UNIVERSITÉ DU QUÉBEC À MONTRÉAL

INFLUENCE À L'ÉCHELLE DU PAYSAGE DES LEGS ASSOCIÉS À L'AMÉNAGEMENT FORESTIER SUR LES ÉPIDÉMIES D'INSECTES.

LANDSCAPE-LEVEL INFLUENCE OF FOREST MANAGEMENT LEGACIES ON OUTBREAKS OF DEFOLIATING INSECTS

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LOUIS-ETIENNE ROBERT

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RÉSUMÉ

La plupart des insectes présents dans les écosystèmes forestiers ne causent pas de dommages significatifs à l'écosystème, mais quelques espèces, comme la tordeuse des bourgeons de l'épinette ou la livrée des forêts peuvent, en stade épidémique, causer d'importants dommages économiques. Malgré l'abondante littérature sur le sujet, beaucoup de questions subsistent sur l'influence des modifications anthropiques à grande échelle sur les patrons d'épidémies. Mieux comprendre cette dynamique entre perturbation anthropique et épidémie d'insecte permettra aux gestionnaires d'être mieux équipés pour prédire les conséquences de leurs politiques d'aménagement.

L'objectif de cette thèse est d'examiner si l'effet des modifications anthropiques à grande échelle suite à l'application de différentes politiques d'aménagement du territoire à un effet sur l'historique des épidémies d'insectes défoliateur. Pour ce faire, nous avons examiné les épidémies de la tordeuse des bourgeons de l'épinette ainsi que la livrée des forêts à travers des reconstructions dendrochronologiques. Cet examen a été réalisé à l'intérieur d'une écorégion se situant à la frontière du Minnesota et de l'Ontario, où les frontières politiques ont créé un contraste entre l'héritage de l'aménagement: récolte à échelle fine au Minnesota, récolte à échelle grossière en Ontario, zone de conservation traversée par la frontière où peu d'aménagements récents ont été effectués.

L'hypothèse sylvicole de la dynamique de la tordeuse des bourgeons de l'épinette postule que l'augmentation de la sévérité des épidémies au siècle dernier est le résultat des conditions forestières créées par l'aménagement. Notre étude supporte

l'hypothèse sylvicole et met en évidence que les effets observables de l'héritage forestier sur la dynamique des épidémies se produisent à l'échelle locale comme à l'échelle du paysage. Nous suggérons aussi que l'aménagement, étant corrélé avec la proportion et la configuration d'hôtes, a modifié le paysage et changé la dynamique temporelle des épidémies de tordeuse de bourgeons de l'épinette. Finalement, nous démontrons les mérites d'une expérience naturelle à l'échelle du paysage offrant ainsi une alternative aux expériences avec manipulation à grande échelle.

Au sujet de la livrée des forêts, nous avons observé que les caractéristiques d'épidémies sont fortement associées avec la composition forestière courante et les legs forestiers (aménagement forestier). Le peuplier faux-tremble domine les paysages aménagés, car il augmente suite à des coupes forestières, ce qui peut expliquer les épidémies plus sévères et synchrones dans les zones aménagées. Nous avons aussi déterminé que les sous-groupes localisés dans la zone de conservation ont des épidémies désynchronisées en partie à cause d'une petite abondance d'espèce hôtes dans cette zone. L'aménagement forestier influence donc les processus de perturbation à l'échelle du paysage à travers des interactions avec la composition et la structure forestière.

Notre étude démontre clairement que les effets des changements anthropiques associés à l'aménagement forestier à l'échelle du paysage sont réels et qu'il est important de les mesurer dans une variété de conditions forestières. Nos données présentées dans le cadre de cette thèse permettent d'établir que les modifications de la répartition des espèces hôtes dans le paysage ont des effets sur les cycles d'épidémies et qu'il est probable que des modifications à l'échelle du paysage permettent de

moduler les cycles d'épidémies. L'ensemble de nos résultats montre aussi l'importance de considérer l'effet de l'aménagement forestier sur de multiples insectes (ou autres processus naturels).

INTRODUCTION

La plupart des insectes présents dans les écosystèmes forestiers ne causent pas de dommages significatifs à l'écosystème mais quelques espèces, comme la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* Clem.) ou la livrée des forêts (*Malacosoma disstria* Hübner) peuvent, en stade épidémique, causer d'importants dommages économiques (Dale *et al.*, 2001). Ces comportements de fluctuations périodiques dans la densité des populations d'insectes ont été étudiés de manière approfondie comme l'illustre l'abondante littérature sur le sujet (Cooke et Roland, 2000; Gray et MacKinnon, 2006; Myers, 1998; Roland et Taylor, 1997; Royama, 2005; Swetnam et Lynch, 1993). Malgré tout, plusieurs questions subsistent quant à l'influence des modifications anthropiques à l'échelle du paysage sur les patrons d'épidémies. À titre d'exemple, Blais (1983) a observé que les épidémies de la tordeuse ont augmenté en fréquence et en intensité au cours du 20e siècle, car l'aménagement forestier favorise les peuplements de sapin-épinette dans la forêt boréale. Cette observation, aussi appelée l'hypothèse sylvicole, est toujours un sujet d'actualité, car, malgré le fait que des études supportent la notion que les épidémies soient plus synchrones et sévères dans les milieux bioclimatiques où son hôte est abondant (Gray *et al.*, 2000), d'autres études vont dans le sens contraire et démontre la stabilité de la fréquence des épidémies de tordeuses depuis les 400 dernières années (Boulanger *et al.*, 2012). Malgré cette divergence, la notion selon laquelle les patrons temporels d'épidémie sont affectés par les modifications à l'échelle du paysage est présente dans d'autres systèmes d'insectes comme celui de la Livrée des forêts. Chez cette espèce, la fragmentation de la structure forestière diminue la durée des épidémies de la livrée des forêts à grande échelle (Roland, 1993) tandis que la proportion d'espèces hôtes à une échelle plus fine augmente la sévérité de la défoliation (Charbonneau *et al.*, 2012). Au cours des années, nous avons assisté à des changements à grande échelle au niveau de la répartition des espèces hôtes de

plusieurs insectes. Malgré ce constat, ainsi que la documentation de ces changements, les études portant sur l'influence des modifications anthropiques du paysage sur les perturbations naturelles subséquentes telles que les épidémies d'insectes restent peu nombreuses (Carleton et MacLellan, 1994; Cyr *et al.*, 2009).

De multiples facteurs présents à l'échelle du paysage tel que la proportion ou composition des espèces hôtes ainsi que leur configuration peuvent affecter les épidémies. À titre d'exemple, la diversité dans la composition affecte les impacts de plusieurs espèces d'insectes défoliateurs particulièrement lorsque la proportion d'espèces non-hôtes est plus grande que la proportion d'espèces hôtes (Jactel et Brockerhoff, 2007). Chez la tordeuse des bourgeons de l'épinette, les peuplements contenant uniquement du sapin baumier mature sont les plus vulnérables à la défoliation (Hennigar *et al.*, 2008). À l'inverse, une plus grande diversité d'espèces d'arbres phylogénétiquement distantes entraînent une augmentation des habitats pour les espèces parasitant l'insecte et réduisent ainsi la mortalité (Cappuccino *et al.*, 1998).

Les changements à l'échelle du paysage n'amènent pas seulement un changement de proportion, mais aussi de configuration forestière pouvant affecter les cycles des épidémies de plusieurs façons par exemple, en créant des barrières physiques ou chimiques à la dispersion (Jactel et Brockerhoff, 2007). Chez certains insectes tels que l'arpenteuse tardive *(Operophtera brumata* L.*),* l'aménagement forestier fragmente le paysage, ce qui réduit la défoliation dans ces paysages fragmentés (Wesołowski et Rowiński, 2006). Du côté de la livrée des forêts, l'hétérogénéité forestière explique aussi la variation de l'étendue des épidémies (Cooke et Roland,

2000; Roland, 1993; Roland *et al.*, 1998), probablement parce que la fragmentation affecte les organismes parasitant celle-ci (Roland, 2005). Curieusement, ces deux insectes possèdent une faible capacité de dispersion comparativement à d'autres insectes comme la tordeuse des bourgeons de l'épinette, ce qui pourrait être un facteur dans l'effet produit par la fragmentation du paysage.

Plusieurs autres facteurs comme la météo, ou le climat peuvent aussi affecter la dynamique des populations d'insectes (Cooke et Roland, 2003; Régnière, 1996; Royama, 1984). Chez la livrée ainsi que la tordeuse, des hivers froids et des printemps chauds sont corrélés avec le début des épidémies alors que des printemps froids sont plutôt associés aux déclins de populations (Candau et Fleming, 2005; Ives, 1973). De plus, la tordeuse ainsi que la livrée sont vulnérables aux froids extrêmes ou à des variations importantes de température durant les périodes de diapause, pouvant ainsi entraîner un effondrement d'une épidémie sur une grande étendue de territoire (Blais *et al.*, 1955; Cooke et Roland, 2003). Finalement, le froid agit sur les relations entre l'insecte et son espèce hôte en désynchronisant le développement de l'insecte avec les bourgeons de son hôte réduisant ainsi la disponibilité de nourriture (Ives, 1973).

Les épidémies de tordeuse des bourgeons de l'épinette

La tordeuse des bourgeons de l'épinette est un insecte à grande capacité de dispersion

de la forêt boréale s'attaquant principalement au sapin baumier (*Abies balsamea L.*) ainsi qu'à plusieurs espèces d'épinettes (*Picea sp.*). Les principaux hôtes de l'insecte sont, par ordre d'importance, le sapin baumier (*Abies balsamea L.*), l'épinette blanche (*Picea glauca* Moench Voss), l'épinette rouge (*Picea rubens* Sarg.) et l'épinette noire (*Picea mariana* Mill. B. S. P.) (Hennigar *et al.*, 2008). La population de cet insecte est reconnue pour augmenter à des niveaux épidémiques avec une fréquence variant entre 30 et 40 ans ou plus (Blais, 1983; Royama, 1984), ce qui entraîne des effets dévastateurs sur les forêts de sapins baumiers. La dynamique des épidémies de tordeuse des bourgeons de l'épinette est aussi reconnue pour se synchroniser par l'influence de variables indépendantes de la densité (le climat par exemple) (Jardon *et al.*, 2003; Royama, 1984; Williams et Liebhold, 2000) et à des endroits où les mouvements migratoires de l'insecte permettent d'échapper aux facteurs liés au contrôle des populations (Barbour, 1990). La coupe à blanc avec protection de la régénération naturelle augmente la présence dans le paysage du sapin baumier, principal hôte de la tordeuse des bourgeons de l'épinette (MacLean, 1984) et aurait contribué à l'augmentation observée de la sévérité des épidémies (Anderson *et al.*, 1987; Blais, 1983).

Les épidémies de Livrée des forêts

La livrée des forêts contraste avec la tordeuse des bourgeons de l'épinette, car son

cycle épidémique est plus court et elle ne se disperse que sur de faibles distances (Peltonen *et al.*, 2002), la rendant ainsi plus vulnérable aux effets de fragmentation. En effet, la livrée des forêts peut être classée dans la catégorie des spécialistes régionaux qui peuvent changer leur préférence d'hôtes dans différentes parties de leur étendue (Witter and Kulman, 1979). Contrairement à la tordeuse, cet insecte s'attaque aux différentes espèces feuillues comme le peuplier faux-tremble (*Populus tremuloides)* et peut aussi se nourrir du bouleau blanc (*Betula papyrifera)* durant les périodes d'épidémies (Mattson *et al.*, 2001). Les épidémies durent généralement 1 ou 2 années avec un intervalle de récurrence de 10-12 ans (Mattson *et al.*, 2001). Même si la mortalité des arbres associés à cet insecte est rare, il demeure que la défoliation réduit la croissance des espèces hôtes dans les peuplements de peupliers (Stearns, 1997) et contribue à changer la structure de ces peuplements en créant des trouées favorisant d'autres espèces d'arbres comme le sapin baumier (Moulinier *et al.*, 2013). Malgré une capacité de dispersion réduite comparée à la tordeuse, les épidémies de livrée des forêts sont tout de même synchrones sur de longues distances (Peltonen *et al.*, 2002) à l'intérieur de la majorité de sa répartition géographique. Par contre, il existe des exceptions dans le centre et l'Ouest canadien où les épidémies sont asynchrones et apériodiques (Hildahl et Reeks, 1960).

Les épidémies de la livrée sont plus probables dans de larges étendues continues d'espèces hôtes, mais les populations sont plus persistantes dans de petites parcelles (Roland, 1993). De précédentes recherches ont rapporté que la mortalité du peuplier dans des peuplements de peuplier faux-tremble est similaire dans des peuplements non défoliés (Duncan et Hodson, 1958; Hildahl et Reeks, 1960). Par contre, des recherches plus récentes ont démontré une augmentation de la mortalité, mais

plusieurs années après la défoliation (Brandt *et al.*, 2003). La livrée des forêts est aussi affectée par la fragmentation du paysage provoquant des épidémies plus longues donc pouvant causer plus de dommages (Roland, 1993).

L'interaction entre les espèces hôtes et les insectes défoliateurs fait partie des mécanismes contrôlant la dynamique de population et un changement dans la distribution des espèces hôtes à grande échelle pourrait affecter la dynamique des populations d'insectes défoliateurs. Étant donné que les épidémies de la livrée des forêts sont plus fréquentes (10-12 ans) et que la livrée possède une capacité de dispersion beaucoup plus faible (0.8-1 km) (Peltonen *et al.*, 2002) comparativement à la TBE (30-40 ans et > 25 km), ces deux espèces se contrastent très largement au niveau spatial (grande dispersion vs petite dispersion), mais aussi au niveau de leur alimentation. Pour ces raisons, celles-ci fournissent un contraste idéal pour examiner cette relation qui existe entre la structure du paysage et son impact sur les cycles épidémiques. De plus, nos aménagements forestiers actuels semblent favoriser le peuplier faux-tremble, comme en témoignent de nombreuses recherches sur l'enfeuillement (Carleton et MacLellan, 1994), ainsi que le sapin qui sont les deux hôtes primaires de ces insectes (Blais, 1983). Mieux comprendre cette dynamique permettra aux gestionnaires d'être mieux équipés pour prédire les conséquences de leurs politiques d'aménagement.

Objectif

L'objectif de cette thèse est d'examiner si l'effet des modifications anthropiques à l'échelle du paysage suite à l'application de différentes politiques d'aménagement du territoire à un effet sur l'historique des épidémies d'insectes défoliateurs. Cet objectif principal doit être vu comme un moyen d'accumuler des données historiques sur les perturbations comme, par exemple, à travers des outils de reconstitution dendrochronologique, tout en abordant le lien qui existe entre les patrons spatiaux d'espèces hôtes ainsi que les variations spatio-temporelles de la dynamique des épidémies d'insectes à grande échelle. Ultimement cette thèse pourra être utilisée afin d'informer les pratiques d'aménagements forestiers qui, si appliquées à l'échelle du paysage, pourraient atténuer ou augmenter l'impact de différents insectes.

Pour atteindre cet objectif, nous avons comparé 2 insectes ayant différentes capacités de dispersion dans un paysage où l'aménagement forestier a affecté la configuration et la proportion des espèces hôtes des 2 insectes. Nous devons d'abord déterminer s'il est possible d'observer des différences dans les cycles temporels d'un insecte à grande capacité de dispersion, c'est-à-dire la tordeuse de bourgeons de l'épinette, et ce, à l'échelle du paysage. Le chapitre 1, intitulé « Effects of forest management legacies on spruce budworm (*Choristoneura fumiferana*) outbreaks » s'attaque à cette question à travers une reconstitution de l'historique des épidémies de tordeuses des bourgeons de l'épinette dans trois zones d'aménagement différentes (extensive, intensive et conservation).

Dans le deuxième chapitre, nous tenterons de déterminer quels facteurs affectent les patrons temporels des épidémies d'un insecte défoliateur à grande dispersion. Ce

deuxième chapitre, intitulé « Landscape effects of forest legacies on spruce budworm outbreaks : A large-scale reconstruction of spruce budworm outbreak history. » s'appuie sur le premier chapitre et a pour objectif de reconstituer les épidémies de tordeuse de bourgeons de l'épinette sur une plus grande étendue de territoire, mais toujours parmi les trois zones d'aménagement forestier précédemment nommées. Ceci permet un test plus explicite du degré d'association entre la tordeuse des bourgeons de l'épinette et plusieurs facteurs explicatifs comme le climat, la configuration et la proportion d'espèces hôtes ce qui, ultimement, nous permettra de statuer sur les effets des modifications du paysage sur les cycles épidémiques de cet insecte.

Dans le chapitre 3, nous tentons de déterminer si les effets des facteurs ayant l'effet le plus important sur les patrons temporels de la tordeuse (chapitre 2) sont robustes lorsqu'appliqués à un autre insecte à plus faible dispersion. Le chapitre 3, intitulé « Influence of land management legacies on forest tent caterpillar (*Malacosoma disstria* Hübner » a donc été effectué dans la même aire d'étude que les deux chapitres précédents, mais porte plutôt sur une reconstitution des épidémies de la livrée des forêts. Tout comme le deuxième chapitre, nous avons aussi effectué une analyse du degré d'association entre diverses caractéristiques des épidémies et de facteurs explicatifs comme la proportion d'espèces hôtes, des facteurs associés à l'hétérogénéité forestière ainsi que des facteurs reliés au climat.

CHAPITRE I - EFFECTS OF FOREST MANAGEMENT LEGACIES ON SPRUCE BUDWORM *(CHORISTONEURA FUMIFERANA)* OUTBREAKS

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Louis-Etienne Robert

Centre d'étude de la forêt (CEF)
Université du Québec à Montréal
C.P. 8888, Succ. Centre-Ville
Montréal, Québec, Canada
H3C 3P8
Corresponding author; E-mail robert.louis-etienne@courrier.uqam.ca
tel: 514-987-3000 ext 4819

Daniel Kneeshaw

Centre d'étude de la forêt (CEF)
Université du Québec à Montréal
C.P. 8888, Succ. Centre-Ville
Montréal, Québec, Canada
H3C 3P8
E-mail kneeshaw.daniel@uqam.ca;

Brian R. Sturtevant

Forestry Sciences Laboratory
North Central Research Station
USDA Forest Service, 5985, Highway K
Rhinelander, USA
WI 54501
E-mail bsturtevant@fs.fed.us

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2.1 Abstract

The "silvicultural hypothesis" of spruce budworm dynamics postulates that increasing severity of spruce budworm outbreaks over the last century resulted from forest conditions created by past management activities. Yet, definitive tests of the hypothesis remain elusive. We examined spruce budworm outbreak dynamics (synchrony, periodicity, and intensity) in the 20th century using historical reconstruction from tree-ring chronologies sampled within 19 sites in a large ecoregion located on the border of Minnesota and Ontario. The study encompassed three areas affected by contrasting management legacies: a fine-grained area (Minnesota, 6 sites, average cut size = 17 ha), a coarse-grained area – (Ontario, 6 sites, average cut size 10 times that of Minnesota), and a conservation zone (7 sites) with little recent harvest activity overlapping the border. Results suggest important differences in outbreak dynamics between the forest management zones that cannot be explained by differences in climate among sample sites. Budworm outbreaks within the conservation zone were more synchronous, with more trees per site affected and less frequent outbreaks than sites sampled within fine-scale managed areas. Outbreak dynamics within forests managed at coarser scales suggest a mixture of the conservation and fine-scale management zone outbreak patterns. Potential factors affecting differences in the observed outbreak patterns include forest pattern, composition, and age. Our study generally supports the silvicultural hypothesis, and emphasizes that management legacy effects on spruce budworm dynamics should be observable at landscape as well as local scales.

2.2 Résumé

L'hypothèse sylvicole de la dynamique de la tordeuse des bourgeons de l'épinette postule que l'augmentation de la sévérité des épidémies au siècle dernier est le résultat des conditions forestières créées par l'aménagement, mais un test définitif de cette hypothèse reste élusif. Nous avons examiné la dynamique des épidémies de la tordeuse des bourgeons de l'épinette du 20e siècle (synchronisme, périodicité et intensité) par la dendrochronologie, et ce sur 19 sites à l'intérieur d'une écorégion située à la frontière du Minnesota et de l'Ontario, où les frontières politiques ont créé un contraste entre l'héritage de l'aménagement: récolte à échelle fine au Minnesota (6 sites, coupe de 17 ha en moyenne), récolte à échelle grossière en Ontario (6 sites, coupe d'environ 10 fois la taille de coupe moyenne du Minnesota), zone de conservation (7 sites) traversée par la frontière où peu d'aménagements récents ont été effectués. Les résultats suggèrent des différences importantes dans la dynamique des épidémies entre les zones d'aménagement forestier. Ces différences sont difficilement explicables par les différences climatiques entre les sites. Les épidémies de tordeuse de bourgeons de l'épinette à l'intérieur de la zone de conservation étaient moins fréquentes, plus synchrones et avec un plus haut pourcentage d'arbres affectés que la zone aménagée à l'échelle fine. Les épidémies à l'intérieur de la zone d'aménagement grossier suggèrent un mélange de la zone de conservation et de la zone d'aménagement fin. Les facteurs potentiels pouvant affecter la dynamique des épidémies sont la composition, l'age et la configuration des espèces hôtes. Notre étude supporte donc l'hypothèse sylvicole et met en évidence que les effets observables de l'héritage forestier sur la dynamique des épidémies se produisent à l'échelle locale comme à l'échelle du paysage.

2.3 Introduction

Current landscapes are a legacy of disturbances created both by natural and human causes (Turner, 1989). Forest management can radically change ecosystem dynamics thus creating legacy effects that persist for decades (Dale *et al.*, 2001; Spies *et al.*, 1994). Such changes in forest patterns and processes are hypothesized to influence insect outbreaks by affecting landscape abundance and connectivity of susceptible host (Raffa *et al.*, 2008). As an example, clearcutting that protects advanced regeneration increases the proportion of balsam fir (*Abies balsamea*) in the landscape (MacLean, 1984), thereby increasing the abundance and connectivity of host species for the eastern spruce budworm (*Choristoneura fumiferana* Clem.). Researchers have speculated that logging and other management activities (e.g., fire suppression) have interfered with natural succession to increase forest susceptibility to spruce budworm, resulting in observed increases in severity of spruce budworm outbreaks during the 20th century (Blais, 1983; Swetnam and Lynch, 1993). This so-called "silvicultural hypothesis" suggests that the converse is also true, i.e. proactive forest land management could decrease forest susceptibility to spruce budworm outbreaks – however this hypothesis has never been rigorously tested (Miller and Rusnock, 1993).

Eastern spruce budworm is an economically important forest defoliator that readily disperses over long distances (Greenbank *et al.*, 1980) and is well-known for the broad-scale spatial synchrony of its outbreaks. Synchrony of defoliators outbreaks are thought to result from regionally-correlated weather perturbations (Royama, 2005), but may also be influenced by landscape conditions at finer, landscape scales (Candau and Fleming, 2005; Haynes *et al.*, 2009a). Host connectivity may influence outbreak synchrony and limit associated forest damage by affecting defoliator dispersal (Ims *et*

al., 2004), movement of natural enemies from adjacent habitats (Cappuccino *et al.*, 1998; Eveleigh *et al.*, 2007), or both.

The impacts of host connectivity on insect outbreaks have been demonstrated in other insect species. As an example, the winter moth *Operophtera brumata* L. causes less defoliation during outbreaks in management fragmented landscapes (Wesołowski and Rowiński, 2006). Conversely, forest fragmentation led to longer more severe outbreaks in isolated stands containing host species of the forest tent caterpillar (*Malacosoma disstria* Hubn.) (Cooke and Roland, 2000; Roland, 1993; Roland *et al.*, 1998). While previous studies have investigated the effects of landscape composition on budworm impacts (Cappuccino *et al.*, 1998; MacKinnon and MacLean, 2004), no studies have been conducted on the effects of landscape pattern on budworm outbreak dynamics. The lack of study is perhaps due to the challenge of locating sufficiently large landscapes that differ with respect to land management but are similar with regard to weather gradients, forest composition, and other potentially confounding factors.

In this paper we address the silvicultural hypothesis by contrasting spruce budworm outbreak patterns within a large (2 million ha) ecoregion containing three different forest land management legacies: a conservation zone (no active management), a fine-grained forest management zone with small cutblocks (17 ha average), and a coarse-grained forest management zone with large cutblocks (an order of magnitude larger). Our hypotheses are two-fold: 1. outbreaks should be more synchronous and last longer in more connected natural forests in the conservation area as they have higher host connectivity and stand susceptibility compared to younger and more fragmented managed landscapes; 2. spruce budworm outbreaks should be more synchronous and of longer duration within coarse-grained managed areas with larger

patches containing host species than within fine-grained managed areas.

2.4 Study Area

The study area is defined by the Border Lakes ecoregion (BLE: 1 870 000 ha) where political boundaries have resulted in starkly contrasting management legacies (Fig. 1). The combination of harvest regulations, road networks and land ownership created a fine-scale pattern of harvesting on the Minnesota side of the Border Lakes ecoregion with harvest units averaging 17 ha from the 1930's to 1990 (Host and White, 2003). In contrast harvest units on the Ontario side of the BLE are an order of magnitude larger (Rempel *et al.*, 1997; Suffling *et al.*, 2003). Harvest rates over the last three decades were relatively similar between the managed zones of Minnesota and Ontario (B.R. Sturtevant, unpublished data, 2010). Between the two managed zones lies a conservation zone formed by Quetico Provincial Park in Ontario and the Boundary Water Canoe Area Wilderness in the United States. Although partial harvesting occurred in the past within the conservation area, clearcut harvesting was uncommon and all harvesting was permanently banned by the 1960's. To confirm the different legacies, we evaluated the average patch size (regardless of disturbance type) from remote sensing data of land cover maps in 1980 and 1990. Before evaluating the average, patch size distributions were area-weighted where the frequency of a patch of a given size observation was multiplied by the number of disturbed cells within the patch. We used weighted patch size distributions to reflect the relative likelihood of selecting a patch of a given size when randomly selecting a disturbed forest cell from the map. For the conservation zone, the average patch size was 13.34 ha (STD = 19.14). The coarse-grained Ontario zone had higher number of

larger patches with an average patch size of 271.12 ha (STD = 440.17) and the fine-grained Minnesota area had an average patch size of 31.91 ha (STD= 42.78). Figure 2 also shows the similarity between the amount of land disturbed per time-period for both the coarse-grained zone and the fine-grained zone. In comparison, the conservation zone has been subject to less disturbance than the other managed areas.

The three management zones shared a common early management history. Region-wide forest harvest activity started at the end of the nineteenth century and focused on selective harvest of the "big pines" (*Pinus strobus, P. resinosa*) using waterways across the majority of the BLE. This was followed in the 1910's by a campaign of fire suppression that may have varied both in efficacy and time of application depending upon the region (Heinselman, 1973). After World War II, the broad use of heavy machinery for clearcut pulpwood harvesting and transportation by road was common on both sides of the border and signaled the beginning of modern industrial forestry. It was during this modern pulpwood era that management activities diverged among zones.

The forest matrix in the three study regions tends towards a coniferous mixed forest. Studies conducted in the Boundary Waters Canoe Area concluded that, since 1910, decreasing fire frequency has changed the dominant pathway of succession from even-aged jack pine (*P. banksiana*) and aspen (*Populus* spp.) to an uneven age structure with a complex mixture of spruce (*Picea spp.)*, paper birch (*Betula papyrifera*), and balsam fir (Frelich and Reich, 1995). In the absence of fire, small scale disturbances like wind, insects and senescence have become the main disturbances, with the notable exception of a major blowdown event that occurred very recently (Mattson and Shriner, 2001). The managed part of the landscape contains similar forest types but has a higher dominance of early successional forest

classes due to forest management operations (Wolter and White, 2002).

2.5 Methods

2.5.1 Data Collection

Spruce budworm outbreaks were reconstructed using tree-ring chronologies of white spruce (*P. glauca*). White spruce rather than balsam fir was selected because of its greater longevity and its higher probability of surviving spruce budworm defoliation (Hennigar *et al.*, 2008). A total of 19 sites were located within mesic forest types to account for the potentially confounding effect of local environment on the dendronological reconstruction. These sites were separated into northern and southern areas within each zone to compare outbreak characteristics at different latitudes as a proxy for climatic conditions and also to compare differences in outbreak parameters within zones (Fig 1). Northern sites in the conservation area were of the same approximate latitude as southern sites in the coarse-grained zone whereas southern sites in the conservation area are even further south (by 12 km) than southern sites in the fine-grained zone. Northern and southern sites in the conservation area were separated by 75 km. Sample sites were selected for ease of access in stands located alongside roads or, in the roadless wilderness, along river corridors and lakeshores. Suitable stands were selected when 5-15 canopy white spruce were located from the road/river. While sampling, we avoided stands located on high slope or very humid areas. All sampled white spruce had a minimum of 30 cm DBH and we sampled two cores taken at a perpendicular angle at 1 meter height from a minimum of at least 5

host trees per site. At least 15 non-host trees from stand located from the roads/river (*P. banksiana* and *P. resinosa* of at least 30 cm DBH) were also cored at one site within each management zone (with the exception of the conservation zone where 15 trees where cored for the northern and southern sites respectively) to serve as a comparison to host chronologies. Cores were stored in plastic straws to be later mounted and sanded (80, 150, 220 grit size).

2.5.2 Tree Ring Chronologies

Tree-ring widths were measured using a Velmex uni-slide measuring table with an accuracy of 0.001 mm connected to a computer (Velmex Incorporated, Bloomfield, New York, USA). We visually crossdated cores within tree and sites and used the program COFECHA (Holmes, 1997) to locate missing or false rings. Tree chronologies were aggregated by northern and southern part of each management zone and an additional COFECHA test was conducted to correct previously undetected errors at the site level and eliminate problematic series. Index chronologies were calculated using the program ARSTAN (Cook, 1985; Holmes, 1997) with a cubic smoothing spline to detrend the series and remove the age-related trend in growth (Cook, 1985). The spline parameters were set to a 50% frequency response cutoff of 60 years (Bouchard *et al.*, 2006; Boulanger and Arseneault, 2004). From 36 to 44 trees were used to develop mean chronologies for each of the three management zones and Table 1 provides summary statistics for the northern and southern part of each management zone.

2.5.3 Outbreak Reconstruction

A spruce budworm outbreak was defined for a given tree ring chronology when a growth reduction was observed for more than 5 years with at least one year where the reduction was greater than 1.28 standard deviations using the program OUTBREAK (Holmes and Swetnam, 1996). This software has been used extensively in various spruce budworm outbreak reconstruction studies (Bouchard *et al.*, 2006; Boulanger and Arseneault, 2004). These thresholds should be sufficient to detect outbreaks of the spruce budworm and avoid confounding potential consequences of other defoliating insect. We are not aware of other defoliator species capable of causing growth reductions of sufficient magnitude in spruce to be identified as an outbreak in this region (W. Mattson US Forest Service (retired), personal communication, 2010). This method has been widely used in researching past spruce budworm outbreaks (Blais, 1983; Jardon *et al.*, 2003; Morin, 1994). Outbreak detection with the program OUTBREAK was more efficient when applied solely to host species (Bouchard *et al.*, 2006). Thus non-host chronologies were only used to validate detected outbreaks by visual comparison of the growth pattern during outbreak and non-outbreak years. Since non-host chronologies were introducing errors in the outbreak reconstruction, we validated our historical reconstruction using aerial survey data from 1910 to 2000 in a 1 km buffer around each dendrochronological sites. We examined the correspondance between the two datasets as shown in figure 2.3 which indicate that the reconstruction is accurate for the conservation zone but a lag between survey data and the reconstruction for the other managed zones is present in the most recent outbreak.

Output from the program OUTBREAK was converted to a frequency graph to show the percentage of trees affected by each outbreak. Results were aggregated by each management zone and north/south groupings to evaluate our hypotheses and to ensure

a reasonable number of tree replicates to define a given outbreak event. For the purpose of analysis, outbreaks were defined as occurring when the number of trees showing a growth reduction exceeded 25%. We found this value to allow an appropriate balance between identifying low intensity outbreaks while minimizing the risks of including false outbreaks. We performed a an additional sensitivity analysis by systematically varying this threshold value between 20% and 50% to evaluate the degree to which our conclusions were dependent on our definition of an outbreak.

Outbreak dynamics were characterized according to their relative spatial synchrony, periodicity, duration and intensity. Synchrony, defined as spatial covariation in population density fluctuation (Bjørnstad *et al.*, 1999) measures the degree of lag between outbreaks occurring in different areas. We used the degree of overlap in outbreaks between northern and southern sites within management zones as a relative indicator of spatial synchrony. Periodicity is the average interval between outbreaks which we measured as the mean time period between the first year of successive outbreaks (Blais, 1983). Intensity is often linked to population density and duration, for our study we used the highest percentage of affected trees for each outbreak as a proxy to evaluate intensity. We also evaluated duration as the number of years an outbreak lasted using our 25% cut-off definition of an outbreak.

2.5.4 Evaluation of Confounding Factors

The premise of our study is that forest management through its effect on forest fragmentation and composition will affect spruce budworm outbreaks among the

different management zones. Different landscape structures of forests resulting from different management legacies (Minnesota: 17 ha cutblocks, Ontario: cutblocks 10 times the average of Minnesota, Conservation: No large-scale harvesting) have previously been established (James, 2010; Wolter *et al.*, 2008). To assess our premise, we measured forest composition both locally (local forest measurements were made using a metric factor 2 prism) and using remote sensing maps of basal area within 1 km neighborhoods (for balsam fir and for spruce spp. Spruce spp. were agglomerated since remote sensing was not specific enough to distinguish between white spruce and black spruce) for each dendrochronology sample site (Wolter *et al.*, 2008). However, it is important to note that these measurements represent current composition at the site selected for the presence of old white spruce. Hence the local (i.e., plot-scale) composition was expected to be biased toward higher white spruce content relative to the broader landscape. For this reason, the 1 km neighborhoods more accurately describe current composition for the study sites. The plot level composition is, however, expected to best reflect local composition effects on spruce budworm outbreaks. For example, Campbell (2007) showed that although there was a weak effect of composition out to 1 km, the strongest composition effect occurred in the local stand and tree neighbourhoods. A nested MANOVA test was performed (North/South nested within zones) to detect differences in forest composition between sites and ANOVA Tukey comparisons were performed when significant statistical differences were found. Current composition has, however, likely changed over the last century, i.e., the period for which outbreak patterns were estimated and thus results should be interpreted prudently for effects in the past.

Climatic Variation

Our sampling design, was stratified by latitude to control for the influence of climate on spruce budworm outbreaks. Our assumption is since sites are located in close proximity, the variation of climatic variables between sites should not be biologically meaningful. Since latitude is not a perfect proxy for climate we summarized ten key climatic variables that have been shown to influence budworm outbreaks and tested that assumption.

We summarized ten key climatic variables (December, January, February and May average and minimum mean monthly temperature along with mean May and July precipitation) that have been shown to influence budworm outbreaks (Campbell, 2007; Candau and Fleming, 2005; Candau and Fleming, 2011; Swetnam and Lynch, 1993). Interpolated weather records were calculated for each year over the last century (1901-2000) using the geographic locations of each dendrochronoloy plot (McKenney *et al.*, 2006). A nested MANOVA (North/South nested within zones) was performed to assess differences between sites and ANOVA Tukey comparisons were performed when significant statistical differences were found.

2.6 Results

2.6.1 Outbreak Reconstruction

The recurrence interval of spruce budworm outbreaks in the conservation zone was estimated to be 23 years with average outbreak duration of 10 years, based on the

25% threshold of trees showing a growth reduction used to define outbreaks (Table 2.2). Four main outbreaks were detected in this zone over the last century: from 1917 to 1922, from 1932 to 1936, from 1958 to 1969, and from 1984 to 1999 (Fig 2.4). The outbreak pattern was clear and well defined with over 60% of the sampled white spruce trees in the conservation zone undergoing significant growth reductions during peak outbreak years with the exception of the 1932 outbreak.

The coarse-grained zone (Ontario) presented a recurrence interval of 32 years with average outbreak duration of 15 years (Table 2.2). Data from the coarse-grained management zone (Ontario) indicated three main outbreaks during the 20th century (Fig 2.4). The first outbreak in the coarse-grained area started earlier than the chronology could detect but ended around 1928 and two other outbreaks can be identified from 1954 to 1963 and from 1983 to 2005.

In the fine-grained area (Minnesota), the recurrence interval for spruce budworm outbreaks was 14 years with outbreak duration of 7 years (Table 2.2). The fine-grained area experienced three main outbreaks that were well defined. One of these outbreaks ended in 1919, another one occurred from 1928 to 1938 and the last occurred from 1995 to 2003 (Fig 2.4). Additionally at least 4 smaller outbreaks were detected in between these last two. These outbreaks mainly occurred from 1949 to 1955, 1958 to 1966, 1971 to 1977 and 1987 to 1991.

The number of outbreaks was similar for the coarse-grained and conservation zones (Table 2.2) while outbreaks were almost twice as frequent in the fine-grained zone. Duration was not similar between these zones but instead was similar between the conservation and fine-grained zone. The conservation zone thus seems to be less

affected by outbreaks (i.e. few and of short duration) than the managed zones where outbreaks were either more frequent or lasted longer. However, it should be noted that outbreaks observed in the coarse grained zone were more severe whereas outbreaks in the fine-grained zone were of lower intensity.

2.6.2 Sensitivity Analysis

To verify whether the 25% cutoff of the number of trees showing a growth reduction led to robust results, we conducted a sensitivity analysis in which the cutoff percentage was varied. The number of outbreaks observed by zone was generally insensitive to the threshold criteria (% trees affected) used to define outbreaks, with the clear exception of the fine-scale management zone (Table 2.2). This result is consistent with the observation of lower intensity outbreaks within that zone since a much lower number of outbreaks were detected with the 50% threshold. Average duration of outbreaks was stable with respect to the threshold criteria for the conservation and fine-scale management zones, but declined with increasing threshold percentage of affected trees for the coarse-scale management zone (Table 2.2). The general pattern that the fine-scale management zone had more frequent but less intense outbreaks of shorter duration than the other two zones was consistent across thresholds ranging from 20-30%, but not at the highest threshold value examined (50%). Outbreak statistics differed consistently between the coarse-grained zone and the conservation zone at threshold values across the same range of values, but were most distinctly different at lower threshold values (20 and 25%).

2.6.3 Outbreak Synchrony

Separation of tree chronologies by latitude suggests that outbreak patterns in the northern and southern sites of the conservation zone were similar and well synchronized (Fig 2.5a) despite a difference in latitude of 75 km. However, the patterns observed at sites at the same latitude but in different zones were dissimilar. For example, the northern conservation and southern coarse-grain sites were at the same latitude but outbreaks at these sites were not synchronous (Fig 2.5a,b). Similarly the southern conservation site, although being located at a latitude intermediate between the two fine-grained sites, did not exhibit an outbreak pattern similar to either. Outbreaks occurring in the northern part of the coarse-grained zone also occurred in its southern part but at a lower intensity suggesting partial synchrony across this zone. Outbreaks in the southern sites of the coarse grained zone were of lower intensity but had an outbreak recurrence interval similar to the fine-grained intensive zone. The earliest recorded outbreaks within the southern and northern sites of the fine-grained zone were synchronous, however, the outbreaks occurring between 1945 and 1985 were not synchronous despite their relatively close proximity (10 km) (Fig 2.5c). The last outbreak (1995-2005) occurred synchronously in both northern and southern sites. Both the northern and southern sites of the fine-grained zone showed a pattern of frequent, low-intensity outbreaks.

2.6.4 Evaluation of Confounding Factors

Forest composition

At the local scale, the amount of live host trees varied from 20% to 65% but a higher percentage of host tree basal area was observed in the conservation north, coarse north and fine south zones (Fig. 2.6a). MANOVA analysis of remotely sensed data at the 1 km scale indicates that the proportion of balsam fir differs between zones ($p=0.0001$) but currently has very low abundance across all zones within the landscape (1-4% of total basal area). The largest compositional difference between zones is for spruce species ($p=0.0001$), which are most abundant within the conservation zone (26-30% by basal area), but which make up a similar proportion of the forest across the two actively managed zones (2-10%) (Fig 2.6b). Deciduous content measured for its potentially protective effect against budworm outbreaks was not significantly different between zones or sites at different latitudes within zones ($p=0.3377$).

Climate

A nested MANOVA (North/South nested within zones) shows that average and minimum winter temperatures (December, January and February) in the southern conservation zone were warmer than all other sites whereas winter temperature in the northern coarse zone were the coldest. Precipitation in May and July were similar for all sites except for the conservation zone which received less precipitation than both the coarse and fine-grained zones. The conservation zone also experienced colder springs (May temperature) in comparison to the actively managed zones. However despite some significant differences in the weather data among zones, their respective mean values from 1900-2000 do not vary substantially (Table 2.3), suggesting that at

our study scale, such weather differences have minor influence, if any, on the widely divergent spruce budworm outbreak behaviours observed across the different management zones.

2.7 Discussion

Our study lends support to the notion that management legacies that modify forest conditions can overcome regional drivers of outbreak synchrony. Outbreaks at the 25% affected tree threshold were more synchronous in the conservation zone relative to the two managed zones despite the considerable difference (75 km) of latitude between the northern and southern sites within this zone. By comparison sites separated by a shorter latitudinal difference in the managed zones, showed a lack of synchrony in outbreak occurrence. We observed this lack of spatial synchrony, despite the fact that outbreaks of defoliators are commonly synchronized across regions by minor but regionally-correlated perturbations (such as weather events) (Bjørnstad *et al.*, 1999; Bjørnstad *et al.*, 2008) - a phenomena known as the Moran effect (Moran, 1953). Further, we observed a lack of synchrony at sites located at similar latitude but within differently managed zones. Very slight differences in climate occurred between the sample sites, but no consistent relationship between climatic variables and outbreak dynamics could be observed. We therefore conclude that observed differences in outbreak behaviour resulted from differences in legacies of past management activities, rather than from distance in space or climatic drivers.

Recent analyses of aerial survey data indicate that geographical variations in forest conditions may influence defoliator outbreak synchrony and temporal dynamics

(Bellier *et al.*, 2007; Candau and Fleming, 2005; Haynes *et al.*, 2009b). Processes such as dispersal by larvae and adults (Johnson *et al.*, 2004) or spatial movements of natural enemies (Cappuccino *et al.*, 1998; Eveleigh *et al.*, 2007; Roland and Taylor, 1997) may influence population dynamics at a scale that is intermediate between stand and regional scales. Our results suggest that management legacies may have affected spruce budworm outbreaks within managed areas and desynchronized spruce budworm outbreaks relative to the conservation area where the combination of fire suppression, historic removal of pines, and lack of recent harvest has left a legacy of older, spruce-dominated forest relative to managed forests (Heinselman, 1996) (Fig. 2.6b). Unlike analyses of aerial surveys, our study minimized the confounding influence of environment and climate by focusing on a single ecoregion where differently managed zones were in close proximity.

Though outbreak synchrony is often correlated with outbreak intensity (i.e., impacts) we observed subtle but important deviations from that general pattern. The intensity of outbreaks (as indicated by the average of highest percentage of affected trees for each outbreak using the 25% threshold) (Table 2.2), was highest in the coarse-grained managed zone and lowest in the fine-grained managed zone. We also observed twice as many outbreaks within the fine-grained management zone (Minnesota) relative to the other two zones (Table 2.2), which decreased the recovery period of the forest. Outbreak duration is most correlated with actual damage to the forest, as multiple years of defoliation are generally required to kill the most vulnerable host species (i.e., balsam fir; (MacLean, 1980)). We found that the average outbreak duration at the 25% threshold within the coarse-grained management zone (Ontario) was roughly double that observed in the fine-grained zone. These results suggest trade-offs between different indicators of forest impacts in the two managed zones with either short-lived but frequent outbreaks of low intensity or long lasting but infrequent

outbreaks of high intensity. By contrast, outbreaks in the conservation zone were both infrequent, of short duration, with intensities intermediate to the two managed zones.

Outbreak dynamics were less consistent between northern and southern sites of the coarse-grained managed zone relative to the other two zones. We had hypothesized that the degree of outbreak synchrony within this zone would be intermediate to that observed within finely-fragmented managed areas of Minnesota (asynchronous) and the relatively unfragmented areas in the conservation zone (synchronous). Instead we found divergent outbreak behavior within the coarsely fragmented Ontario zone, where data from southern sites indicated behaviour more similar to that observed in the fine-grained zone and northern sites indicated behaviour more similar to the conservation zone (Fig. 2.5). One potential explanation for this pattern is that harvest disturbances in Minnesota are more evenly distributed in time and space, whereas the more clustered harvest pattern in Ontario resulted in greater spatial heterogeneity in fragmentation, leading to divergent behaviour. Alternatively, harvest was more recent in the vicinity of the northern sites of the coarse-grained zone and thus, effects on outbreak behavior may not yet be manifest. The greater abundance of white spruce plantations particularly in the south east toward Lake Superior might be a further explanation but they are scattered in the study area and could thus be expected have a limited impact. A last possibility is that the southern sites are influenced by their close proximity to a large lake (Fig. 2.1). Cappucino *et al.* (1998) observed lower budworm damage on forested islands within lakes relative to forests within a land matrix. Analyses across a greater range of locations throughout the Border Lakes Landscape, currently underway, will provide stronger insights into the effects of management legacies and other landscape features on budworm outbreak dynamics.

Observed divergences in budworm outbreak behaviour begs the question: at what spatial scale is fragmentation perceived by the spruce budworm? A detailed study of a European defoliator, winter moth *Operophtera brumata* L. which has a smaller dispersal capacity than the spruce budworm, found that fragmentation created by management increased dispersal mortality during outbreaks and may explain why less defoliation is experienced in fragmented landscapes (Wesołowski and Rowiński, 2006). Spruce budworm adults can disperse long distances (i.e., 10's to 100's of km) during outbreaks (Greenbank *et al.*, 1980), suggesting that this species may be less sensitive to fragmentation of host species than the less mobile winter moth. Yet dispersal of adults is only one process of many that may influence outbreak dynamics (Régnière and Nealis, 2007). For example, Cappuccino *et al.* (1998) found that stands of budworm hosts isolated at the scale of 1 km neighborhoods experienced less damage than host species surrounded by forest dominated by host during an outbreak in Quebec, Canada.

Spatial influences on the natural enemy complex may have influenced the response time of budworm enemies in managed areas of the border lakes ecoregion to the point that outbreak dynamics were affected. The larger patch size of the coarse-grained zone may have created a lag in the response of natural enemies (Cappuccino *et al.*, 1998). This would result in higher intensity and longer lasting outbreaks in this zone since spruce budworm population growth would be initially favored due to the lack of predators (Cooke *et al.*, 2007). In contrast, we suspect that the natural enemy response may be more rapid in the fine-grained zone due to its lower mean patch sizes. If so, then this reduced lag time may have contributed to the observed lower intensity but frequent outbreaks observed there. However, while the different legacies of forest management are evident in disturbance patch sizes and forest age observed across zones, corresponding differences in patterns of budworm host are far less

obvious. This suggests that repeated budworm disturbances may have degraded this pattern over time (James, 2010). Since our composition dataset represents only a snapshot of current composition, additional temporal data on age structure and abundance of host species is needed to discriminate between effects of host proportion, configuration, and age structure on spruce budworm outbreak dynamics.

2.7.1 Potential Climatic Influence

Climate is known to affect outbreaks and it is conceivable that some of the differences observed in the current data could be explained by differences in climate between sites (Campbell *et al.*, 2006; Volney and Fleming, 2000). Our study design aimed to control the effect of climatic variability by allowing us to compare sites in different zones but in close proximity and by explicitly considering northern and southern sites within zones. Winter temperature can limit the survival of second instar larvae (Candau and Fleming, 2005) and, as expected, northern latitude sites were consistently colder than southern latitude sites nested within management zones. If winter temperature had a significant influence over outbreak dynamics, we should have observed consistent budworm outbreak dynamics at similar latitudes – yet this was not the case. The most consistent climatic difference between management zones was the relatively colder springs and lower May-July precipitation observed within the conservation zone. If the slightly colder springs in this zone were to affect outbreaks then we would have expected them to limit the duration and intensity of spruce budworm outbreaks compared to the other management zones. If there was an effect of the slightly drier beginning of summer it would be to increase outbreak intensity as early summer moisture affects the beginning of the initial phase of

outbreaks (Lucuik, 1984). Instead the most severe outbreaks were observed within northern sites in the coarse-grained zone, an area with higher July precipitation. Such inconsistencies in pattern, when combined with the minor absolute differences in climate between zones relative to the divergent outbreak behavior observed, suggests that, at the scale of this study, climate is at best a minor factor underlying observed differences in outbreak behavior.

2.8 Conclusion

Our study is among the first to show that forest management can influence dynamics of outbreaks. A review of previous studies conducted at stand-scales found no evidence to support the notion that stand-level treatments by themselves have any influence on defoliator outbreaks (Muzika and Liebhold, 2000). Our study suggests that the cumulative effects of management at the landscape scale can modify spruce budworm outbreak patterns. Management legacies have changed the patch structure and the contiguity of older forests, and potentially the composition of those forests. We observed clear differences between outbreak patterns in managed and unmanaged forests irrespective of distance and position between sample locations. Our results suggest that, although the elimination of budworm outbreaks is unlikely to be achieved via forest management practices, such practices may influence the scale, periodicity, or duration of the outbreaks. It appears a trade-off exists between frequent outbreaks of short duration versus less frequent but higher intensity outbreaks, and that landscape-scale management legacies can influence realization of these two outbreak behaviors.

Miller and Rusnock (1993) suggested that evaluation of the silvicultural hypothesis may be beyond the limits of classic scientific method due to the long term and large-scale experiments required to perform an adequate test of the hypothesis. Such an experiment is currently underway (Volney *et al.*, 1999), however, it will be decades before any conclusions may be made. Landscape-scale "natural experiments" such as presented here offer a complimentary method that, in lieu of true large-scale controlled experiments, may be effectively applied to understand drivers underlying outbreak dynamics at scales relevant to the outbreak process.

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2.11 Tables and Figures

Table 2.1 : COFECHA output of summary statistics (mean ring width, sensitivity and inter-tree correlation) of the dendrochronological reconstruction for the northern and southern part of each management zone.

					Sensitivity		
Lattitude	Zone	No. of trees	Time Span	Mean Ring Width (mm)	Mean	SD	Intertree Correlation
North	Conservation	20	1906-2005	2.51	0.268	1.356	0.643
South	Conservation	24	1897-2005	1.93	0.277	1.026	0.604
North	Fine	22	1903-2005	2.45	0.277	1.363	0.63
South	Fine	22	1920-2005	2.87	0.263	1.508	0.61
North	Coarse	19	1895-2005	2.34	0.28	1.157	0.604
South	Coarse	17	1932-2005	2.45	0.272	1.159	0.571

Table 2.2 : Changes in the number of outbreaks, their duration, their recurrence and their intensity across landscapes with different land-use based on different threshold criteria for the determination of outbreaks (20, 25, 30 and 50%). Note that the value used in this study is 25%.

	Number of outbreaks				Average Duration (yr.)				Recurrence Interval				Avg. Intensity (max % of trees affected)			
	Threshold				Threshold				Threshold				Threshold			
	20	25	30	50	20	25	30	50	20	25	30	50	20	25	30	50
Conservation	4	4	3	3	10.75	9.75	10.33	8	22.67	23	34	35	61.44	61.44	72.95	72.95
Coarse	3	3	3	4	17.67	15.33	11.67	5.25	32	33	31.5	27.33	66.67	66.67	66.67	65.39
Fine	9	7	5	2	7.33	7.57	7.4	5	10.25	13.67	20.5	63	39.04	43.79	49.5	63.15

Statistics are for corrected outbreak data (outbreaks of 1-2 years in duration have been supressed/integrated to other outbreaks)

Table 2.3 : Mean weather data and their standard deviation for each management zone. (Source of data: McKenney *et al.* (2006))

		May precipitation (mm)		July precipitation (mm)		Dec Temperature (°C)		Dec min Temperature (°C)		Jan Temperature (°C)		Jan min Temperature (°C)		Feb Temperature (°C)		Feb min Temperature (°C)		May Temperature (°C)		May min Temperature (°C)	
Latitude	Zone	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std
North	Conservation	92.4	0.4	91.6	0.3	-13.0	0.1	-18.5	0.1	-16.9	0.1	-23.5	0.1	-14.1	0.0	-21.4	0.1	9.2	0.1	2.0	0.0
South	Conservation	95.2	0.2	92.7	0.1	-12.0	0.1	-17.2	0.1	-15.7	0.1	-21.9	0.1	-13.0	0.0	-19.9	0.0	9.0	0.1	2.0	0.1
North	Fine	97.4	0.2	93.6	0.2	-12.9	0.0	-18.1	0.0	-16.9	0.0	-23.0	0.0	-13.8	0.0	-20.6	0.0	10.4	0.0	3.4	0.0
South	Fine	97.3	0.3	93.0	0.2	-12.6	0.0	-18.0	0.0	-16.5	0.0	-22.9	0.0	-13.4	0.0	-20.5	0.0	10.2	0.0	2.9	0.0
North	Coarse	97.1	0.5	93.5	1.2	-13.1	0.6	-18.3	0.4	-17.1	0.7	-23.2	0.4	-14.0	0.7	-20.8	0.4	10.1	0.1	3.1	0.1
South	Coarse	97.6	0.3	93.7	0.3	-12.9	0.4	-18.3	0.2	-16.9	0.6	-23.1	0.3	-13.7	0.6	-20.7	0.3	9.9	0.1	2.7	0.4

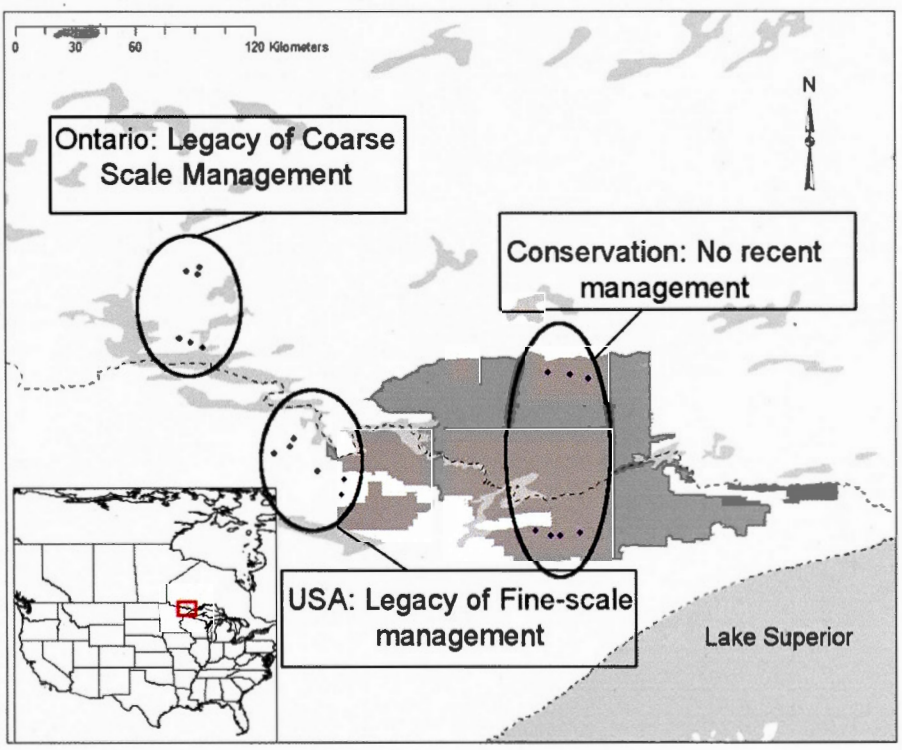

Figure 2.1 : The Border lakes landscape study area located at the border between Ontario (Canada) and Minnesota (United States). Points represent sampling sites for dendrochronological reconstructions of outbreaks.

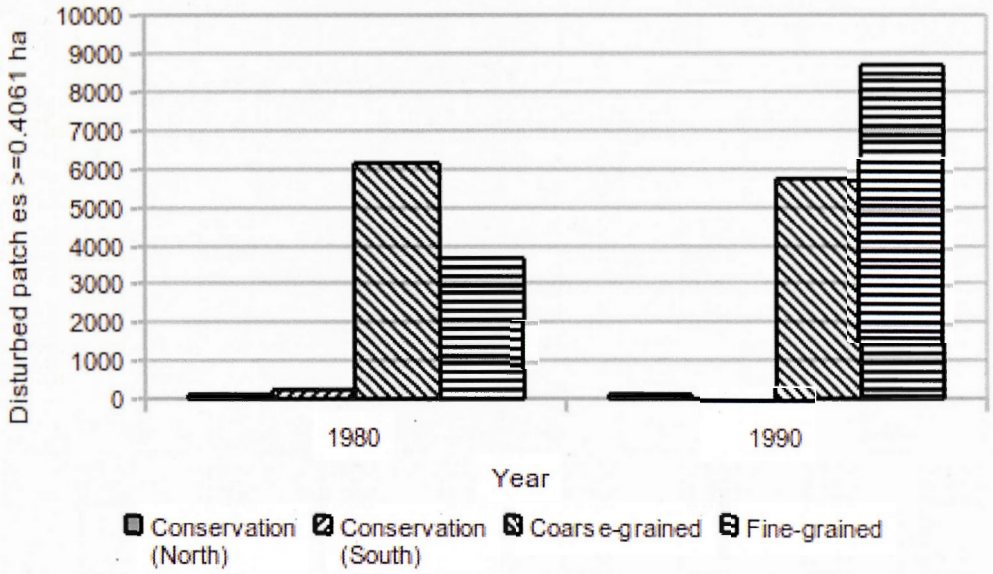

Figure 2.2 : Summary graph of land-cover remote sensing showing the quantity of disturbed patches in ha. that are larger or equal to 0.4061 ha from 1980-1990. Disturbance refer to all disturbances (fire, harvest, insect, wind) based on a change from a forested state to a non-forested state between image dates in the time-series.

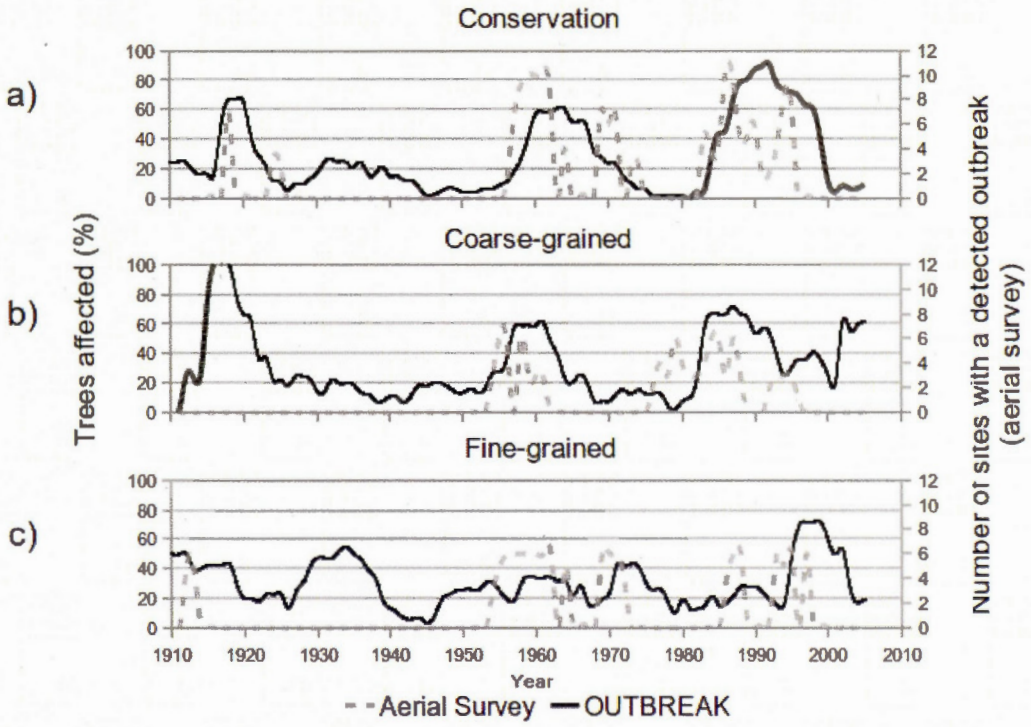

Figure 2.3 : Comparison between the frequency graph from OUTBREAK and the aerial survey data taken at a 1 km buffer around each dendrochronological sites. Left axis represent the output from OUTBREAK and right axis represent the number of sites experiencing outbreak for a given year.

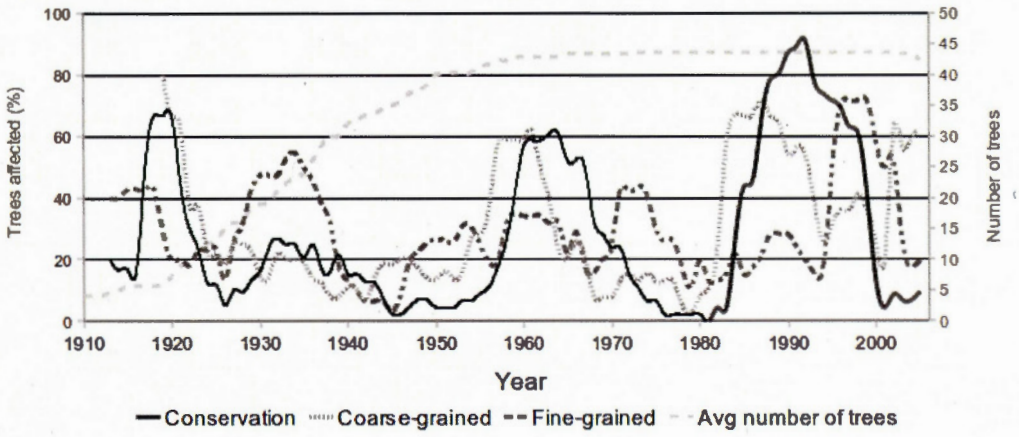

Figure 2.4 : Frequency graph of the percentage affected trees of the program OUTBREAK aggregated by management zones (Conservation, Coarse-grained, Fine-grained) (shown in the left axis). The right axis shows the number of trees available for each year of the reconstruction.

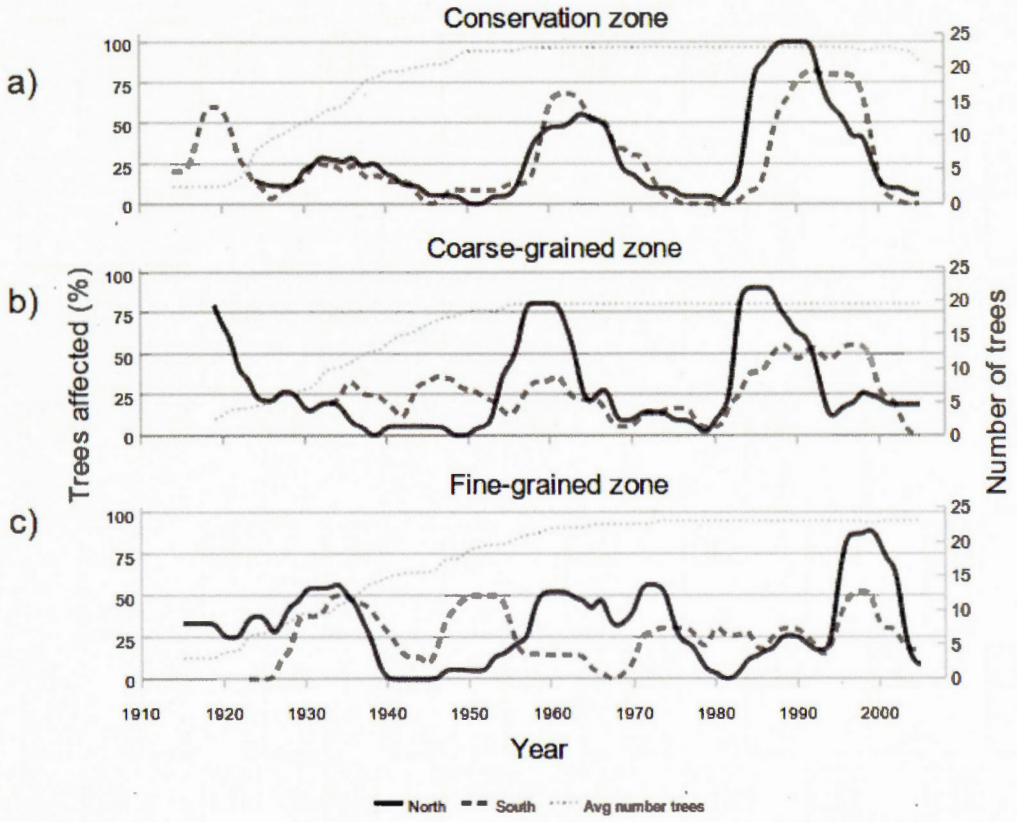

Figure 2.5 : Frequency graph of the program OUTBREAK showing north and south percentage of affected tree for each management zones (Conservation, Coarse-grained, Fine-grained) (shown in the left axis). Average number of trees for each zones (shown in the right axis) was 23 per year except for prior to 1950.

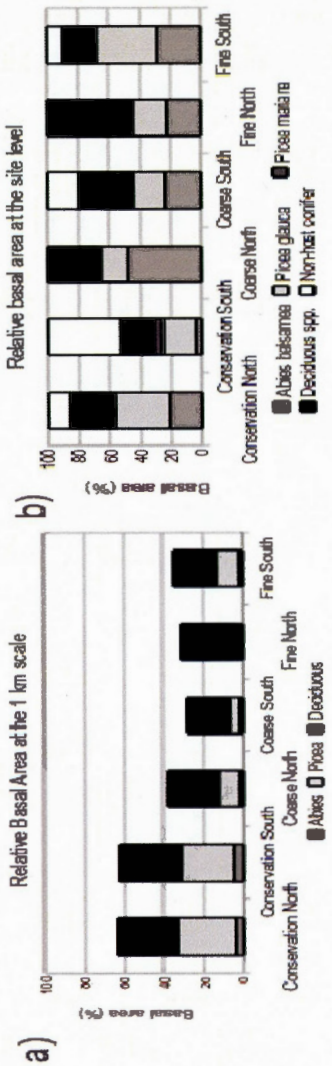

Figure 2.6 : Difference in local forest composition for each management zones at a) 1 km scale from remote sensing and b) at the site scale from local inventory.

CHAPITRE II - LANDSCAPE EFFECTS OF FOREST LEGACIES ON SPRUCE BUDWORM OUTBREAKS: A LARGE-SCALE RECONSTRUCTION OF SPRUCE BUDWORM OUTBREAK HISTORY

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Louis-Etienne Robert

Centre d'étude de la forêt (CEF)
Université du Québec à Montréal
C.P. 8888, Succ. Centre-Ville
Montréal, Québec, Canada
H3C 3P8
Corresponding author; E-mail robert.louis-etienne@courrier.uqam.ca
tel: 514-987-3000 ext 4819

Brian R. Sturtevant

Institute for Applied Ecosystem Studies
Northern Research Station
USDA Forest Service, 5985, Highway K
Rhinelander, USA
WI 54501
E-mail bsturtevant@fs.fed.us

Patrick M. A. James

Département des sciences biologiques
Université de Montréal
C.P. 6128, succursale Centre-ville
Montréal, Québec, Canada
H3C 3J7
E-mail patrick.ma.james@umontreal.ca

Barry J Cooke

Canadian Forest Service
Northern Forestry Centre
5320–122nd Street
Edmonton, Alberta, Canada
T6H 3S5
E-mail: bcooke@nrcan.gc.ca

Daniel Kneeshaw

Centre d'étude de la forêt (CEF)
Université du Québec à Montréal
C.P. 8888, Succ. Centre-Ville
Montréal, Québec, Canada
H3C 3P8
E-mail kneeshaw.daniel@uqam.ca;

Keywords Border Lakes; Spruce budworm; harvest disturbance; Landscape Ecology, forest management legacies.

3.1 Abstract

Evidence is mounting that the cumulative effects of land management (i.e., management legacies) observed at landscape scales can affect defoliator outbreak dynamics in time and space. However, the extent to which historical management legacies dominate outbreak dynamics of irruptive insect species in relation to other factors such as climate and local forest composition is not clear. Our objective was to assess the extent to which spatial legacies affected spatial variation in temporal patterns of spruce budworm outbreaks within a large ecoregion on the border of Canada and the United States where management policies have created different forest legacies. The study area encompassed three zones affected by contrasting management legacies: a fine-grained zone (Minnesota), a coarse-grained zone (Ontario), and a wilderness zone with little recent harvest activity overlapping the border. We examined spruce budworm outbreak patterns using tree-ring chronologies to reconstruct the outbreak history of 16 subgroups distributed in the study area. Using time-series clustering and variance partitioning alongside remotely sensed forest structure and climatic data, we identified significant variation in temporal outbreak patterns among geographically separated regions that have different histories of forest management. Our partition of variance demonstrated that forest configuration explained 14% of the variance whereas the climatic variables and forest proportion explained 0.2% and 11% of the total variance respectively. Cluster analysis supports the notion of a management effect on the spatio-temporal patterns of spruce budworm outbreaks. At the scale of our study, we suggest that management has modified the landscape and influenced host proportion and configuration which changed the temporal patterns of spruce budworm outbreaks to higher frequencies/lower intensity outbreak in more fragmented subzones containing lower proportion of host. Our study also shows the merit of a natural landscape-scale experiment which offers an alternative to large-scale controlled experiments.

3.2 Résumé

Récemment, une accumulation de preuves scientifiques a permis d'établir que l'effet cumulatif des legs forestiers laissés par l'aménagement à l'échelle du paysage affecte la dynamique des insectes défoliateurs. Par contre, le degré avec lequel l'historique des legs de l'aménagement forestier domine la dynamique éruptive des épidémies d'insecte par rapport à d'autres facteurs tels que le climat et la composition forestière locale est encore sujet à discussion. Notre objectif était d'examiner l'étendue de l'association entre les legs forestiers et la variation spatio-temporelle des épidémies de la tordeuse de bourgeons de l'épinette à l'intérieur d'une écorégion. L'aire d'étude se situe à la frontière du Minnesota et de l'Ontario, où les frontières politiques ont créé un contraste entre l'héritage de l'aménagement: une récolte à échelle fine au Minnesota, une récolte à échelle grossière en Ontario et une zone de conservation traversée par la frontière où peu d'aménagements récents ont été effectués. Nous avons examiné les patrons des épidémies de tordeuse en utilisant une reconstitution dendrochronologique de celles-ci sur 16 sous-groupes distribués dans notre aire d'étude. En utilisant des analyses de groupements pour série temporelle ainsi qu'une partition de la variance sur des données de télédétection de la structure forestière et des données climatique, nous avons identifié une variation temporelle significative des épidémies entre les régions possédant un historique d'aménagement différent. Notre partition de la variance démontre que les zones d'aménagement expliquent 14 % de la variance tandis que les variables climatiques et la condition forestière courante expliquent 0.2% et 11% de la variance, respectivement. Notre analyse de groupement supporte aussi la notion d'un effet des zones d'aménagement sur la dynamique spatio-temporelle des épidémies de tordeuse de bourgeons de l'épinette. À l'échelle de notre étude, nous suggérons que l'aménagement a modifié la proportion et la configuration d'arbres hôtes dans le paysage, et ainsi, changé la dynamique temporelle des épidémies de la tordeuse de bourgeons de l'épinette vers une dynamique plus fréquente/moins intense dans les sous-groupes plus fragmentés et possédant une plus petite proportion d'hôtes. Nous démontrons aussi les mérites d'une expérience naturelle à l'échelle du paysage offrant ainsi une alternative aux expériences avec manipulation à grande échelle.

3.3 Introduction

Forest disturbances such as fire, logging and insect outbreaks leave legacies that can facilitate or constrain future disturbances by modifying landscape structure (proportion and configuration) (James *et al.*, 2007; Turner, 1989). Disturbances interact and through these interactions can amplify or attenuate each other or change the probability of their occurrence (Turner, 2010). For example, Blais (1983) observed an increasing trend in the severity and frequency of spruce budworm outbreaks and attributed its cause to extensive logging which favored stands of fir-spruce on the landscape. This observation, termed the silvicultural hypothesis, has however never been directly supported due to the complexity of doing manipulative experiments at the landscape level (Miller and Rusnock, 1993). Nevertheless, understanding how land management legacies affect other disturbance processes remains of central importance to sustainable forest management because of the potential large-scale impacts of these disturbances (Dale *et al.*, 2001).

The eastern spruce budworm (*Choristoneura fumiferana* Clem., hereafter SBW) is an economically important forest defoliator that is capable of long-distance dispersal (Greenbank *et al.*, 1980). SBW is well-known for the broad-scale spatial synchrony of its outbreaks (Jardon *et al.*, 2003) which is thought to result from regionally-correlated weather perturbations (Royama, 2005) (i.e. The Moran effect), but may be influenced by landscape structure at finer, landscape scales (Candau and Fleming, 2005). Among possible factors influencing synchrony, host connectivity may limit associated forest damage by affecting defoliator dispersal (Ims *et al.*, 2004), movement of natural enemies from adjacent habitats (Cappuccino *et al.*, 1998;

Eveleigh *et al.*, 2007), or both. Recently however, Robert *et al.* (2012) demonstrated that spruce budworm outbreaks within unmanaged forest landscapes tend to: 1) be more synchronous, 2) have more trees per site affected, and 3) are less frequent than within managed areas. However, the extent to which historical management legacies influence large scale outbreak dynamics relative to other factors such as climate and local forest composition is not clear. Here we extend the qualitative analysis of Robert *et al.* (2012) to a quantitative analysis of a more extensive dataset.

In this study we evaluate the extent to which spatial legacies affected spatial variation in temporal patterns of spruce budworm outbreaks within a large (6 million ha) ecoregion containing three divergent forest management zones with contrasting forest structure. We hypothesize that the temporal pattern of outbreaks inferred by tree-ring analysis was strongly affected by divergent management activities occurring in the different forest management zones, such that outbreak patterns were more similar within than among management zones. Factors underlying such a response could include differences in landscape structure (i.e., host abundance, hardwood content, host configuration) and age structure of the surrounding forests through their influence either on natural enemy communities or dispersal losses (Su *et al.*, 1996) which could promote high frequency/low intensity outbreaks in areas with a low proportion or fragmented pattern of hosts. We therefore evaluated the extent to which current forest structure in the neighborhood of the study sites explain differences in outbreak behavior, with the recognition that current forest attributes do not necessarily reflect past conditions during any given outbreak. We evaluate the relative importance of forest configuration, forest proportion, and climate to explain spruce budworm outbreak patterns across the study area.

3.4 Methods

3.4.1 Study area

Our study area centers on a large (6 million ha) ecoregion located at the international border between the state of Minnesota (USA) and the province of Ontario (Canada) (Fig. 1). The whole study area shared a common early management history. Region-wide forest harvest activity started at the end of the 19th century and focused on selective harvest of the "big pines" (*Pinus strobus*, *Pinus resinosa*) using waterways across the majority of the Border Lakes Landscape. Forest harvest patterns diverged sharply between Minnesota and Ontario approximately 50 years ago, coinciding with mechanized clear-cutting operations (primarily for pulpwood) on both sides of the border. In particular, clearcuts within managed Canadian forests were roughly an order of magnitude larger in size than managed American forests to the south, though the rate of harvest was similar in both areas (James *et al.*, 2011a; Sturtevant *et al.*, 2014). Between these managed regions lies an approximately 1 million ha wilderness area that includes Quetico Provincial Park in Ontario and the Boundary Waters Canoe Area Wilderness in Minnesota where no timber harvest has occurred since the early 1970s (Heinselman, 1996).

The study area lies within the transition zone between the Great Lakes-St. Lawrence mixedwood and boreal forest regions (Fig. 3.1). Its geomorphology is characteristic of the Canadian Shield, typified by a high density of lakes and wetlands (Superior Mixed Forest Ecoregional Planning, 2002). Forest composition within the ecoregion boundaries is best characterized as mixed "near boreal" (Heinselman, 1973) forest

with a high proportion of boreal tree species i.e.: jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), tamarack (*Larix larcinia*), as well as tree species near the northern limit of their range (e.g., white pine (*Pinus strobus*), red pine (*Pinus resinosa*), red maple (*Acer rubrum*). Further north composition becomes more boreal and conifer-dominated, while further south the composition becomes more temperate and deciduous-dominated (Sturtevant *et al.*, 2014). Studies conducted in the Boundary Waters Canoe Area concluded that, since 1910, decreasing fire frequency has changed the dominant pathway of succession from even-aged jack pine and aspen spp. to an uneven-aged structure with a complex mixture of spruce spp., paper birch, and balsam fir (Frelich and Reich, 1995). The managed part of the landscape contains similar forest types but has a higher dominance of early successional forest classes due to forest management operations (Wolter and White, 2002) thus creating a contrasting host pattern partially corresponding to the border of Minnesota, Ontario and Wilderness zones (James *et al.*, 2011b).

3.4.2 Historical reconstruction of spruce budworm outbreaks

Sampling design

We reconstructed spruce budworm outbreak history using tree-ring analyses of old white spruce tree cores sampled from 51 sites distributed across the study area (Fig.

3.1). These study sites were located according to a stratified sampling design to account for variation attributed to land management legacies (zones) and dominant climatic gradients. Land management zones were defined as "fine" (fine-scale managed forests in Minnesota labeled as "F"), "coarse" (coarse-scaled managed forests in Ontario, labeled as "C"), and "wilderness" (the wilderness area defined by the Boundary Waters Canoe Area and the Quetico Provincial Park, labeled as "W"). Sites within each land management zone were divided into 2 to 3 longitudinal groups of sites spanning the east-west extent of the study area. Longitudinal groups were further separated into northern and southern subgroups represented by a minimum of three sample sites with an average of 8 km between sites. Two additional subgroups were located in the North and South extremes of the wilderness land area. Throughout this article, labels are thus identified using a management-zone-longitudinal zone-latitudinal zone terminology (Example: Coarse-Western-North or CWN). Longitudinal groups and latitudinal subgroups were defined to maintain similarity in the scale of area represented by each respective grouping. This sampling scheme was designed to maximize our ability to separate climatic effects from land management legacy effects within the constraints of the management zone boundaries.

Spruce budworm outbreaks were reconstructed using tree-ring chronologies of white spruce (Robert *et al.*, 2012). White spruce rather than balsam fir was selected because of its greater longevity and its higher probability of surviving spruce budworm defoliation (Nealis and Régnière, 2004). Sample sites were selected for ease of access in stands located alongside roads or, in the roadless wilderness, along river corridors and lakeshores. Suitable sites were selected based on the presence of 5 to 15 old, canopy white spruce located on flat or midslope topographic positions characterized by mesic growing environments (see Table 3.1 for detailed distribution of sampled

trees among subzone). We sampled two cores at one meter height from a minimum of at least five host trees per site that were greater than 30 cm Diameter at Breast Height (DBH). A minimum of 15 non-host trees (jack pine and red pine; > 30 cm DBH) per longitudinal groups were also cored at sample sites. Cores were stored in plastic straws and were later mounted and sanded using progressively finer grit sizes (80, 150, and 220).

Tree ring chronologies

Tree-ring widths were measured using a Velmex uni-slide measuring table with an accuracy of 0.001 mm connected to a computer (Velmex Incorporated, Bloomfield, New York, USA) and cross-dated within individual tree and sites with the program COFECHA (Holmes, 1997) to locate missing or false rings and to test for measurement errors. Tree-ring chronologies were aggregated into their respective subgroups and an additional COFECHA test was conducted to correct previously undetected errors at the site level and eliminate problem series. Index chronologies were calculated using the program ARSTAN (Cook, 1985; Holmes, 1997) with a cubic smoothing spline to detrend the series and remove age-related trend in growth (Cook, 1985). The spline parameters were set to a 50% frequency response cutoff of 60 years (Bouchard *et al.*, 2006; Boulanger and Arseneault, 2004). Between 13 and 24 trees were used to develop chronologies for each subgroup (Table 3.1).

Outbreak reconstruction

A spruce budworm outbreak was defined for a given single tree-ring chronology when a growth reduction was observed for more than 5 years, with at least one year where the reduction was greater than 1.28 standard deviations from the mean. We used the program OUTBREAK (Holmes and Swetnam, 1996), which has been used extensively in various spruce budworm outbreak reconstruction studies and has been found to be sufficient to detect outbreaks of the spruce budworm while avoiding confounding consequences of other defoliating insects (Bouchard *et al.*, 2006; Boulanger and Arseneault, 2004). We note that no other defoliators of consequence are known in the region that are capable of causing sufficient growth reductions of a number of years to be identified as an outbreak (W. Mattson, US Forest Service (retired), personal communication, 2010). Outbreak detection using the program OUTBREAK was more efficient when applied solely to host species (Bouchard *et al.*, 2006). Thus non-host chronologies were only used to validate detected outbreaks by visual comparison of the growth pattern during outbreak and non-outbreak years.

Output from the program OUTBREAK was converted to frequency graphs to show the percentage of trees affected by each outbreak. Outbreaks from these frequency graphs were identified when the number of trees that showed a growth reduction exceeded 25%. This value was used as a benchmark to define outbreak characteristics since it was previously found to allow an appropriate balance between identifying low intensity outbreaks while minimizing the risks of including false outbreaks (Robert *et al.*, 2012). As with Robert *et al.* (2012), we performed an additional sensitivity analysis by systematically varying this threshold value between 20% and

50% to evaluate the degree to which interpretations were dependent on our definition of an outbreak. Outbreak characteristics were generally insensitive to the threshold criteria (% of trees affected) used to define outbreaks (Table 3.1). Outbreak dynamics were characterized at all thresholds by periodicity, duration and intensity as defined in Robert *et al.* (2012). Periodicity is the average interval between outbreaks which we measured as the mean time period between the first year of successive outbreaks (Blais, 1983). Intensity is linked to population density and duration (Régnière and You, 1991) which results in greater growth reduction in host trees (Swetnam and Lynch, 1989). Therefore we used the highest percentage of affected trees for each outbreak as a proxy to evaluate intensity. We also evaluated duration as the number of years an outbreak occurred using the different outbreak thresholds described above to better understand the consequences of human changes on outbreak dynamics.

3.4.3 Predictor variables examined

Climate

Climate varies both latitudinally along a North-South gradient and longitudinally with distance from Lake Superior, where sites closer to the lake have a more temperate climate than further sites which are more continental (Cooke and Roland, 2000). Climate is also a close proxy for daily weather, which influences daily development rates and survival throughout all life stages of the spruce budworm (Régnière *et al.*, 2012). Therefore, historical climate data in our outbreak pattern analysis were

included using seasonal temperature (winter, summer, spring) and annual precipitations. We used minimum monthly averages of temperature based on interpolated weather records using the geographic locations of each study site calculated for each year over the last century (1901-2000) (McKenney *et al.*, 2006). We calculated an average mean minimum temperature for winter (November to February), spring (March to June), summer (July to October) using similar methodology as in Swetnam *et al.* (1993) and used the 100 year average for each subzones in our analysis (Table 3.2).

Forest Structure

We hypothesized that spatial variation in outbreak temporal patterns could be affected by variation in surrounding forest structure. To assess the effect of forest proportion and age, we extracted from Landsat-based estimates (*circa 2004*) to calculate the average relative basal area of host (spruce spp. and balsam fir) and deciduous trees within a variable radius ranging from a variable site radius (0.5, 1, 5, 10, 20, 30, 40 and 50 km; Table 3.2) to assess the potential effect of different scale of measurement of these variables on the insect-host relationship (Campbell, 2007; Wolter *et al.*, 2008). We also included forest age structure data through a similar methodology based on a time series (1975-2000) of a remotely sensed LANDSAT classification map originating from Wolter *et al.* (2012). For this dataset, forested pixels of each site that changed to more open land cover classes during the timespan of our dataset were assumed to be [younger than 1975] whereas the rest of forested pixels were classified

as [older than 1975]. Thus predictors included for our forest proportion hypothesis are the average percentage of host/deciduous trees as well as the percentage of forests older/younger than a 1975 stand origin at variable radius around each sites (Table 3.2). It is important to note that these measures represent current composition at sites selected for the presence of old white spruce and composition has likely changed over the last century, i.e. the period for which outbreak patterns were estimated. For our forest configuration hypothesis, we included the mean patch size and the number of patches calculated through FRAGSTAT (McGarigal *et al.*, 2002) of Landsat classification map data (Wolter *et al.*, 2012) representing forested and open cover classes at a variable radius around each site (0.5, 1, 5, 10, 20, 30, 40 and 50 km; Table 3.2).

3.4.4 Statistical analysis

We evaluated the degree of similarity among subgroups to visualize spatial patterns in temporal outbreak variation using temporal cluster analysis. If management legacies had an effect on outbreaks, we should see an obvious spatial clustering by management subgroups. We applied cluster analyses (Keogh and Kasetty, 2003) through both complete linkage and k-means methods with 3 centroids where the output is plotted through a principal component analysis (PCA) using R (R Core Team, 2008). The cluster analysis was based on the annual percentage of trees affected by outbreaks, which assesses the similarity of time-series patterns using an

index of similarity. We chose the Euclidean distance between time-series for its simplicity to implement and because it is widely used as a benchmark index in time-series analysis (Keogh and Kasetty, 2003).

We evaluated the degree of association between annual percent trees affected and our predictor variables (i.e., forest configuration, climate and forest proportion) through variance partitioning. Using a selection of our predictors (Table 3.2) performed through forward selection and linear regression for each of our 3 competing hypotheses, we partitioned the variance among percentage affected trees time-series using redundancy analysis (RDA). Variance partitioning of the RDA solution was undertaken using the "varpart" function in the Vegan package in R (Oksanen *et al.*, 2013). In this variance partitioning, the response matrix was the unscaled annual percentage of affected trees by subgroups and a set of predictors reflecting each hypothesis.

Due to the high total number of predictors in relation to the total number of available subgroups, we required an objective method of selecting the most parsimonious set of predictor variables for our variance partitioning analysis. We performed a forward selection protocol using the R package Packfor (Dray *et al.*, 2013) combined with ANOVA and linear regression to select significant predictors and verify their collinearity with variance inflation factor. The forward selection uses permutation of residuals from an RDA model to include environmental factors into the model (Oksanen *et al.*, 2013). Predictors selected through the stepwise selection protocol for each hypotheses of our variance partitioning included : Forest configuration: Number of upland forest patches at 10 km scale and the mean patch size of upland grass class at 30 km scale; Climate: summer minimum temperature; Forest proportion:

percentage of host at 20 km and 50 km, the average percentage of deciduous spp. at 30 km and average number of pixel classified as younger than 1975. The adjusted R square was used to assess the proportion of variance associated with each partition (Peres-Neto *et al.*, 2006). Variance partitioning allowed us to examine the unique contribution of each predictor and to assess the degree of support for our hypothesized drivers affecting spruce budworm outbreak dynamics in different regions of the Border Lakes Landscape.

3.5 Results

3.5.1 Subgroups Outbreak Statistics

Outbreak characteristic varied as a function of thresholds but the general pattern was fairly robust to variation in definition of thresholds. The general pattern that the fine-scale management zone had more frequent but less intense outbreaks of shorter duration than the other two zones was consistent across thresholds ranging from 20%–30%, but not at the highest threshold value examined (50%) which emphasized high intensity outbreaks. Average duration of outbreaks was stable with respect to the threshold criteria for the conservation and fine-scale management zones but declined with increasing threshold percentage of affected trees for the coarse-scale management zone (Table 3.3). Outbreak statistics differed consistently between the coarse-grained zone and the conservation zone at threshold values across the same range of values but were most distinctly different at lower threshold values (20% and

25%).

Despite the fact that time-series (1928-2005) contained only 2 to 3 cycles, we can distinguish differences in outbreaks characteristics between subgroups at the 25% threshold (Table 3.3). Outbreaks located in the Fine-scale subgroups (Minnesota) had a recurrence interval between 13 and 33 years with a duration of 8 to 15 years (Table 3.3). The number of outbreaks varied from two in the Fine center north subgroup which is the closest subgroup to the Wilderness, to six in the western subgroup. The average intensity varied from 41% to 85% with lower intensity outbreaks found in the Fine center south and Fine western south subgroups. These two subgroups were also characterized by the shortest return interval (13 years), suggesting frequent low intensity outbreaks.

Recurrence interval of outbreaks in the Coarse-scale managed zone were longer and more variable than in the other zones (16-62 yrs) with higher values in the east. Average outbreak duration was between 9 and 16 years (Table 3.3) and from 2 to 4 outbreaks were detected. The largest number of outbreaks occurred in the Coarse western south subgroup and were most similar to the Fine western subgroup. Outbreaks in the Coarse zone were generally of high intensity with 69% to 85% of the trees affected in the peak outbreak year, with the notable exception of the Coarse western south subgroup that had a lower average intensity (41%) of high-frequency outbreaks.

The Wilderness subgroups showed a recurrence interval between 18 and 27 years and a duration of 9 to 13 years (Table 3.3). The Wilderness subgroups had the least variability in outbreak characteristics except in the Wilderness eastern north subgroup which experienced a higher recurrence interval of outbreaks and also underwent one

more outbreak than in the other Wilderness areas. The average intensity varied from 42% to 68% with the highest intensity located in the Wilderness western south subgroups.

3.5.2 Groupings of outbreak patterns

Cluster analyses with both complete linkage and K-means methods (Fig. 3.2) were used to assess the similarity of outbreak patterns amongst subgroups while providing a complementary comparison without *a priori* hypotheses on the factors affecting spruce budworm outbreak patterns. We expected that if the dominant factor determining outbreak pattern was climate or dispersal, subgroups should cluster by spatial proximity, however subgroups clustered in a pattern that partially corresponded to management zone.

The cluster analyses separated the subzones into three main groups. Fine subgroups in the west clustered within the same centroid and separated at the first or second level within the cluster analysis. This corresponds to an outbreak pattern that is more frequent, less intense and of shorter duration than the other zones (Fig 3.2-3.3). The second group contains subgroups in the Coarse management zone, with the exception of the Coarse west south subgroup, and were observed to have the most intense outbreaks. The wilderness cluster encompassed many of the subgroups in the wilderness zone and was characterized by outbreaks that are highly synchronous within the zone (Fig. 3.2-3.3). There is some variation with subgroups being

associated with different management zones such as the Coarse west south subgroup which, despite having an outbreak pattern more similar to Minnesota western groups, clustered with the wilderness cluster. Such groupings however, may be explained by spatial proximity or recent history. Another example can be found in subgroups in the east which clustered together probably due to a low intensity outbreak in the 1950s (Fig. 3.2-3.3).

3.5.3 Climate, forest configuration or proportion?

We tested 3 hypotheses (forest configuration, climate, forest proportion) and interactions between these hypotheses to explain spatial variation in outbreak dynamics. We addressed these hypotheses using variables extracted from forward selection in a variation partition. Variation partitioning resulted in 35% of the total variance explained by the three tested hypotheses (forest configuration, climate, forest proportion) (Fig. 3.4). The forest configuration variables explained 14% of the variance, the climatic variables explained 0.2% of the variance whereas 11% of the total variance was explained by the forest proportion. It is also important to note that the fraction associated with the interaction of forest proportion and climate variables amount to 3% which indicate that the variation of the climate dataset is intercorrelated with variation in forest proportion dataset. This same intercorrelation is present within the fraction representing the association between forest configuration and forest proportion (5%). Thus forest proportion/configuration variables explain most of the variation in spruce budworm outbreak temporal pattern

and climate variables by themselves do not explain much of the variation in outbreak temporal pattern but are mostly associated with forest proportion.

3.6 Discussion

Our study observed a wide range in temporal dynamics of spruce budworm outbreaks – ranging from frequent low-intensity outbreaks in the managed zones to infrequent high intensity outbreaks in the central wilderness zone – within a large landscape containing divergent land management legacies that created different spatial structures of hosts (James *et al.*, 2011b). Over the last 50+ years, forest management has changed landscape structure, forest composition and host connectivity which may have influenced outbreak synchrony and limited associated forest damage. Changed synchrony and forest damage may be due to the influence of changed forest structure on defoliator dispersal (Ims *et al.*, 2004), movement of natural enemies from adjacent habitats (Cappuccino *et al.*, 1998; Eveleigh *et al.*, 2007), or both. Our results demonstrate that forest configuration and proportion resulting from management legacies explains the most variation in outbreak patterns whereas at the scale of the study, climate explains very little of the variation. The observation that landscape scale management can influence insect outbreak dynamics is also supported in other insect species. Insects such as the forest tent caterpillar (*Malacosoma disstria Hubn.*) experienced longer outbreaks in fragmented forests (Cooke and Roland, 2000; Roland, 1993; Roland *et al.*, 1998) and the winter moth (*Operophtera brumata L.*) was found to cause less defoliation during outbreaks in management-fragmented

landscapes (Wesołowski and Rowiński, 2006).

Researchers have speculated that forest management (i.e., logging and fire suppression) has interfered with natural succession to increase forest susceptibility to spruce budworm (Miller and Rusnock, 1993) and that by promoting the availability of large contiguous stands dominated by fir. forest management also promotes vulnerability to spruce budworm (Baskerville, 1975). These changes towards a more vulnerable forest have been suggested to increase the severity of budworm outbreaks during the 20th century (Blais, 1983; Swetnam and Lynch, 1993). It has been demonstrated that higher hardwood content can reduce mortality in host conifer stands (Bergeron *et al.*, 1995; Su *et al.*, 1996). Among the probable hypotheses explaining this lower mortality is that higher parasitism and predation rates occur in more diverse landscapes (Cappuccino *et al.*, 1998). Even though a long term dendrochronological reconstruction found a stable trend in outbreak frequency in southern Quebec (Boulanger *et al.*, 2012), our results tend to agree with Jardon *et al.* (2003) hypothesis that the outbreak dynamics of spruce budworm vary around an underlying pattern within a designated landscape probably due to forest management creating gradients in landscape structure.

Both forest configuration and proportion explained a high percentage of the total variation in our variation partition analysis, it is however surprising that these 2 hypotheses do not share a higher percentage of collinearity. Whereas the different legacies of forest management are evident in disturbances patch size observed across zones (Sturtevant *et al.*, 2014), corresponding patterns of spruce budworm hosts following these disturbances are far less obvious, suggesting that repeated budworm disturbances may have degraded this pattern over time (James *et al.*, 2010; James *et*

al., 2011a). Current host proportion, specifically balsam fir, are likely less reflective of the host proportion found in the early 1930's. Likewise the forest age information is limited to a classification younger or older then 1975. However, we do know that fine-scaled and spatially-diffuse clearcut harvest disturbances have been fairly consistently applied within managed forests of Minnesota since the 1930s (Sturtevant *et al.*, 2014; White and Host, 2008), that the wilderness area has had a lower disturbance rate during the last century than surrounding managed forests (Heinselman, 1996), and that forest clearcut operations in northwestern Ontario tends to be more spatially aggregated and larger in size relative to Minnesota (Sturtevant *et al.*, 2014). The fact that our outbreak time-series clustered partially by management zone and that forest configuration and proportion explain most of the variance in our variation partitioning, support the notion that divergent land management legacies caused measurable differences in outbreak dynamics. For example, in our study the shorter but more frequent outbreaks in the fine-grained zone may be related to its lower mean patch sizes and higher hardwood content (Wolter and White, 2002; Wolter *et al.*, 2008).

Adult dispersal has been proposed as an important mechanism at the stand and regional scales for the synchronization of insect outbreaks (Eveleigh *et al.*, 2007; Johnson *et al.*, 2004; Régnière and Nealis, 2008; Roland and Taylor, 1997) by linking spatially disjunct populations so that cycle phase converges on a single global state (Cooke *et al.*, 2007). Spruce budworm adults can disperse long distances (i.e., 10's to 100's of km) during outbreaks (Greenbank *et al.*, 1980; Sturtevant *et al.*, 2014) and prior analysis of dispersal patterns suggests dispersing budworms are insensitive to landscape patterns of host at the scale of the study landscape (Anderson and Sturtevant, 2011). This suggests that spruce budworm sensitivities to fragmentation of host species do not scale up to the level of landscape-scale outbreak compared to

other insects with smaller dispersal capacity.

However the contrast in outbreak synchrony in wilderness versus managed zones indicates that despite spruce budworm long range dispersal capability, other factors such as management type influence outbreak synchrony. As an example, the wilderness subgroups are spaced far apart (75 km difference latitudinally) but undergo synchronous outbreaks (Fig. 3.3). This contrasts with the fine zone subgroups separated latitudinally by shorter distances but which undergo asynchronous outbreaks. This asynchrony occurs despite the fact that outbreaks are commonly regionally synchronized by correlated perturbations like weather events (Bjørnstad *et al.*, 1999; Bjørnstad *et al.*, 2008). Another potential explanation for the desynchronization in outbreak pattern is that harvest disturbances in Minnesota are more evenly distributed in time and space, whereas harvest pattern in Ontario is more concentrated in specific regions throughout time which means that greater fragmentation occurred only locally at any given time. This provides an explanation to the observed clustering pattern in the Coarse zone which generally clustered together despite their large geographical distance. However, the Coarse western south subgroup did not cluster with other Coarse subgroups but more with Wilderness and Fine subgroups possibly because harvest activity in its vicinity started in the 1980's and thus, effects on outbreak behavior may not yet be manifest.

Climate is also known to affect outbreaks (Campbell *et al.*, 2006; Candau and Fleming, 2005; Gray, 2008; Gray, 2013), and our study indicated that climatic gradients within the study area had a negligible influence on budworm outbreaks (i.e., 0.2% of the variance). We controlled for the longitudinal and latitudinal gradients to the best extent possible given the spatial constraints of the management zones and were able to detect a climatic effect. Use of climate normals rather than weather

observations does not account for finer-scaled perturbations to budworm population dynamics, but it may capture higher-order constraints such as overwintering mortality due to warm temperature (Régnière and Nealis, 2007; Régnière *et al.*, 2012). An examination of the raw data shows that winters, as expected, are consistently colder in northern latitude subgroups. We also observed an East-West gradient in climate possibly due to a lake effect of Lake Superior. As shown by Sturtevant et al., (2014) this east-west gradient is related to slightly warmer summer temperatures and lower precipitation in the west than in the east and these subtle differences may influence population dynamics. There is in fact a tendency of the cluster analysis to show the presence of an East-West gradient with four of the six eastern subgroups clustering together (Fig 3.2a). However, the lower proportion of variation explained by climatic variables in our partition of variance analysis (Fig 3.4) and the lack of east-west groupings in the k-means cluster analysis (Fig 3.2b) suggests that climate is not the dominant factor at the scale of our study but still need to be accounted for within our analysis.

3.7 Conclusion

Miller and Rusnock (1993) suggested that evaluation of the silvicultural hypothesis may be beyond the limits of classic scientific methods due to the impracticality of the long term and large-scale experiments required to adequately test it. However, our study demonstrates that a natural landscape-scale experiment may offer an alternative to large-scale manipulative experiments where we can observe the effect of landscape structure on spruce budworm outbreak patterns. Although more research will be

required to quantify the effect and direction of landscape structure on spruce budworm outbreak dynamics, our study shows that the spatial variation of temporal patterns of spruce budworm outbreaks varies among different landscape forest structures which is, in part, the product of forest management legacies. At the broad spatial scale of our study and using a time-series based approach, we suggest that forest landscape structure can increase the frequency of spruce budworm outbreaks while reducing outbreak intensity in the case of a finer scale management. We also suggest that coarser scale management could increase outbreak intensity. These patterns are confounded by relationships with climatic gradients (especially East-West) but at the scale of this study (6 million ha), climate is not the dominant factor. Instead the cumulative effects of human interventions across the landscape have led to changes in the natural disturbance regime of the spruce budworm. Our findings thus suggest that land management at large scales may have unintended effects on natural processes and that more attention needs to be focused on these landscape-scale effects.

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3.10 Tables and figures

Table 3.1 : COFECHA output of summary statistics (mean ring width, sensitivity and inter-tree correlation) of the dendrochronological reconstruction for all subgroups.

							Sensitivity		
Zone	Group	Subgroup	Idtag	No. of trees	Time Span	Mean Ring Width (mm)	Mean	SD	Intertree Correlation
Coarse	Eastern	North	CEN	18	1849-2005	1.91	0.25	1.13	0.496
Coarse	Eastern	South	CES	22	1883-2005	2.15	0.819	1.024	0.472
Coarse	Western	North	CWN	19	1895-2005	2.34	0.28	1.157	0.604
Coarse	Western	South	CWS	17	1932-2005	2.45	0.272	1.159	0.571
Conservation	Eastern	North	WEN	16	1924-2006	1.81	0.279	1.029	0.661
Conservation	Eastern	South	WES	13	1902-2006	2.19	0.25	1.105	0.506
Conservation	North	North	WWN	20	1906-2005	2.51	0.268	1.356	0.643
Conservation	South	South	WSS	24	1897-2005	1.93	0.277	1.026	0.604
Conservation	Western	North	WWN	21	1836-2006	1.69	0.259	0.92	0.626
Conservation	Western	South	WWS	15	1880-2006	1.62	0.253	0.826	0.594
Fine	Center	North	FCN	21	1915-2005	3.04	0.208	1.351	0.636
Fine	Center	South	FCS	23	1828-2005	3.23	0.207	1.413	0.583
Fine	Eastern	North	FEN	22	1836-2005	2.56	0.238	1.403	0.368
Fine	Eastern	South	FES	22	1872-2005	2.06	0.249	1.075	0.609
Fine	Western	North	FWN	22	1903-2005	2.45	0.277	1.363	0.63
Fine	Western	South	FWS	22	1920-2005	2.87	0.263	1.508	0.61

Table 3.2 : Table containing available predictors for each of our hypotheses.

Distance of evaluation	Hypotheses											
	Forest Configuration				Forest Proportion			Climate				
	Number of patches of Forest (Upland)	Mean Patch Size of Forest (Upland)	Number of patches (Open)	Mean Patch Size (Open)	Host (% basal area)	Deciduous (% Basal area)	% stand older 1975	% stand younger 1975	Spring Minimum Temperature	Summer Minimum Temperature	Winter Minimum Temperature	Annual Precipitation (mm)
Subzone Avg	x	x	x	x	x	x	x	x	x	x	x	x
0.5 km	x	x	x	x	x	x						
1 km	x	x	x	x	x	x						
5 km	x	x	x	x	x	x						
10 km	x	x	x	x	x	x						
20 km	x	x	x	x	x	x						
30 km	x	x	x	x	x							
40 km	x	x	x	x	x							
50 km	x	x	x	x	x							

Predictors that were included into the Variation Partition

Table 3.3 : Changes in the number of outbreaks, their duration, their recurrence and their intensity across landscapes with different land-use based on different threshold criteria for the determination of outbreaks (20, 25, 30 and 50%).

Zone	Group	Subgroup	Idtag	No. of Outbreaks				Average Duration (years)				Average Intensity (Max percentage of trees affected)				Recurrence Interval			
				20%	25%	30%	50%	20%	25%	30%	50%	20%	25%	30%	50%	20%	25%	30%	50%
Coarse	Eastern	North	CEN	2	2	2	1	18	16	16	17	69	69	69	94	52	55	54	57
Coarse	Eastern	South	CES	3	2	2	2	12	15	14	11	59	77	77	77	31	62	59	32
Coarse	Western	North	CWN	6	3	3	3	7	10	8	7	55	84	84	84	16	31	32	
Coarse	Western	South	CWS	4	4	4	1	13	9	7	8	41	41	41	56	16	16	16	
Wilderness	Eastern	North	WEN	3	3	3	1	14	13	9	14	51	51	49	75	25	27	25	
Wilderness	Eastern	South	WES	4	4	2	1	10	9	18	10	43	43	50	54	20	18	27	22
Wilderness	North	North	WNN	3	3	2	2	13	11	14	8	63	63	79	79	27	26	26	28
Wilderness	South	South	WSS	4	4	4	2	12	10	8	8	49	53	53	68	25	23	23	30
Wilderness	Western	North	WWN	5	4	4	2	11	9	10	9	50	50	57	69	22	23	35	37
Wilderness	Western	South	WWS	4	4	3	3	13	10	11	10	68	68	81	81	21	24	36	36
Fine	Center	North	FCN	2	2	3	2	16	15	9	10	85	85	71	85	32	33	22	
Fine	Center	South	FCS	4	5	5	1	12	8	6	4	44	43	43	60	16	14	14	63
Fine	Eastern	North	FEN	3	3	3	2	16	13	11	13	67	67	67	83	35	33	32	41
Fine	Eastern	South	FES	5	4	4	3	13	13	12	10	62	72	72	82	21	28	28	22
Fine	Western	North	FWN	4	4	4	4	15	11	11	6	58	61	60	64	27	25	27	32
Fine	Western	South	FWS	6	6	5	3	8	8	8	4	41	41	43	51	13	13	17	

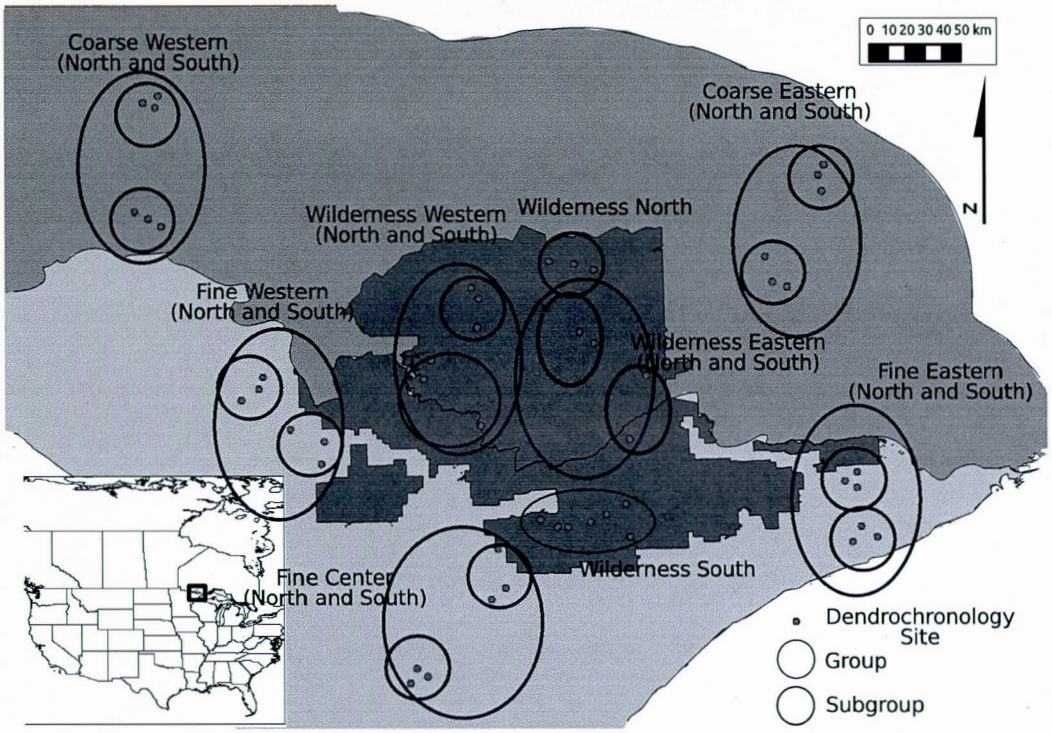

Figure 3.1 : The Border lakes landscape study area located at the border between Ontario (Canada) and Minnesota (United States). Points represent sampling sites for dendrochronological reconstructions of outbreaks.

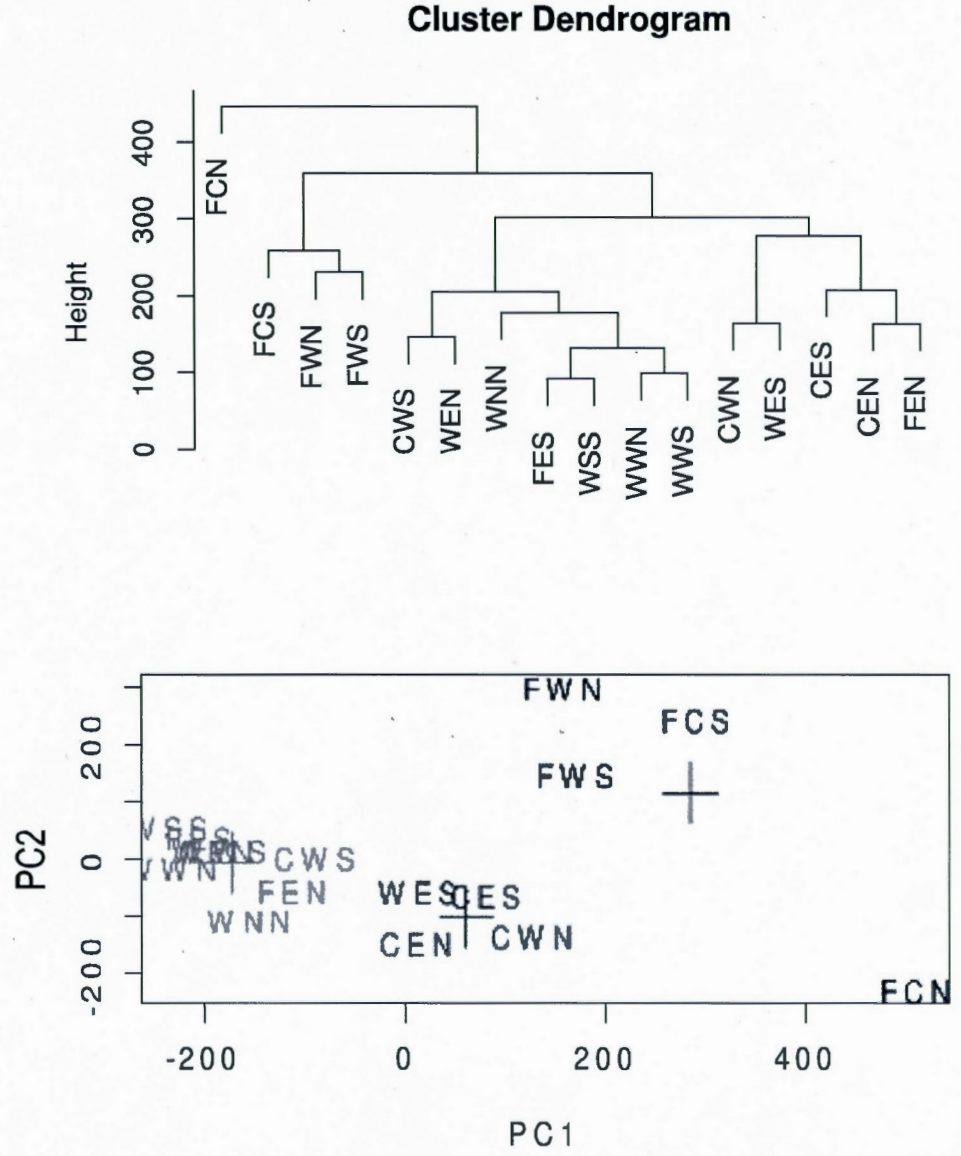

Figure 3.2 : Temporal cluster analysis and PCA representation of k-means cluster analysis using 3 centroids.

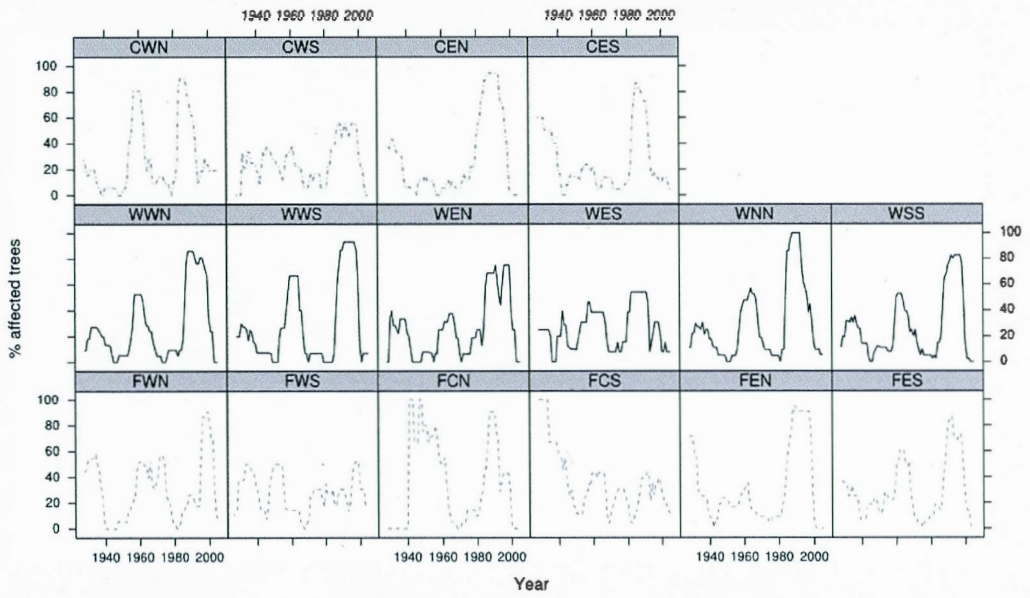

Figure 3.3 : Frequency graph of the program OUTBREAK showing percentage of affected trees throughout time for each subgroups: Wilderness (Black), Coarse-grained (Gray) and Fine-grained (Gray).

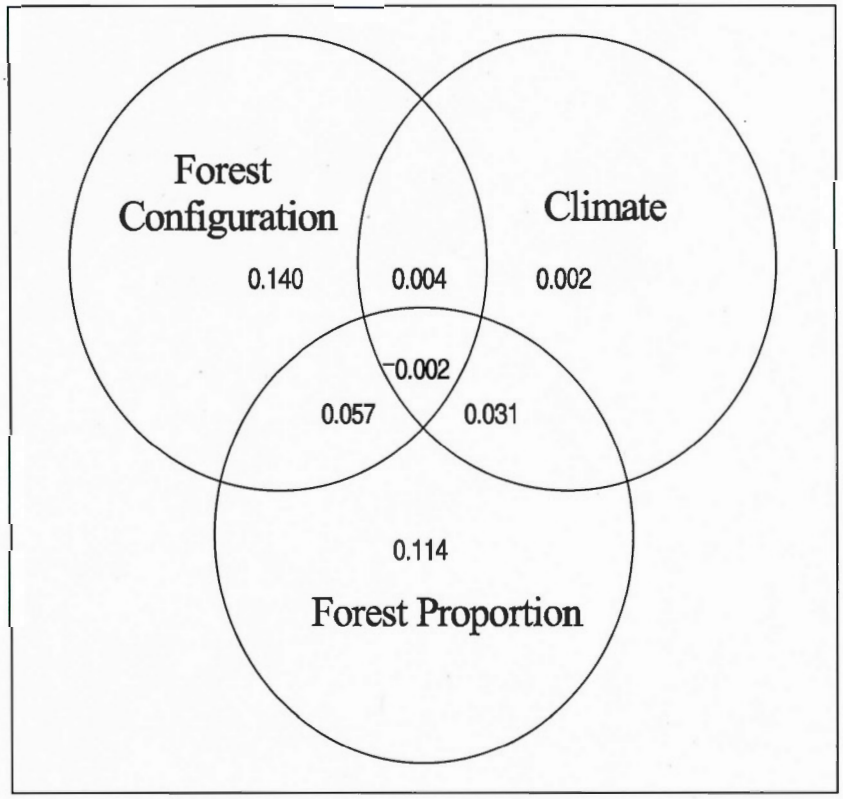

Figure 3.4 : Variation partitioning using predictors chosen by forward selection for each of our 3 hypotheses (Forest Configuration, Climate. Forest Proportion).

CHAPITRE III - INFLUENCE OF LAND MANAGEMENT LEGACIES ON FOREST TENT CATERPILLAR (MALACOSOMA DISSTRIA HUBN.) OUTBREAK DYNAMICS IN THE BORDER LAKES REGION OF MINNESOTA AND ONTARIO.

(Manuscrit en préparation pour publication dans Landscape Ecology)

Louis-Etienne Robert

Centre d'étude de la forêt (CEF)
Université du Québec à Montréal
C.P. 8888, Succ. Centre-Ville
Montréal, Québec, Canada
H3C 3P8
Corresponding author; E-mail robert.louis-etienne@courrier.uqam.ca
tel: 514-987-3000 ext 4819

Brian R. Sturtevant

Institute for Applied Ecosystem Studies
Northern Research Station
USDA Forest Service, 5985, Highway K
Rhinelander, USA
WI 54501
E-mail bsturtevant@fs.fed.us

Barry J Cooke

Canadian Forest Service
Northern Forestry Centre
5320–122nd Street
Edmonton, Alberta, Canada
T6H 3S5
E-mail: bcooke@nrcan.gc.ca

Patrick M. A. James

Département des sciences biologiques
Université de Montréal
C.P. 6128, succursale Centre-ville
Montréal, Québec, Canada
H3C 3J7
E-mail patrick.ma.james@umontreal.ca

Daniel Kneeshaw

Centre d'étude de la forêt (CEF)
Université du Québec à Montréal
C.P. 8888, Succ. Centre-Ville
Montréal, Québec, Canada
H3C 3P8
E-mail kneeshaw.daniel@uqam.ca;

Keywords: Border Lakes, Forest Tent Caterpillar outbreaks, Landscape Ecology, Harvest disturbance, climate influence, proportion of host species, Dendrochronology, forest management legacies

4.1 Abstract

In this study, we investigate the effect of forest structure resulting from divergent land management practices on spatio-temporal patterns of forest tent caterpillar (*Malacosoma disstria* Hubn.) outbreaks. Our objective is to examine the degree of association between spatio-temporal patterns of outbreaks and (1) forest configuration, (2) host proportion and (3) climate. The study area encompassed three zones affected by contrasting management legacies: a fine-grained zone (Minnesota), a coarse-grained zone (Ontario), and a wilderness zone with little recent harvest activity overlapping the border. We reconstructed the spatio-temporal pattern of forest tent caterpillar outbreaks history using dendrochronological analysis of aspen (*Populus tremuloides*) tree cores, the insect's primary host, sampled located in 14 subgroups within the study area. Using time-series clustering and partition of variance analysis we examine the association of outbreak characteristics (i.e. periodicity, intensity, duration) with remotely sensed forest structure and climate data. The variation partition of outbreak characteristics explained 36% of the total variation and were strongly associated with forest configuration (34 %). Forest configuration was correlated with host proportion and the association of forest configuration with climate also accounted for 13% of the variation. Climate variables by themselves had a negative contribution to the partition of variance suggesting that, at this scale, the effect of forest structure dominates. This study also outline that subgroups located inside the wilderness zone had desynchronized outbreaks due, at least in part, to the lower host abundance and more continuous forest in the subgroups of this zone. We propose that early successional fragmented forest dominated by trembling aspen is more present in the managed landscapes due to forest harvesting operation and may thus explain the more severe and synchronized outbreaks in the managed zones.

4.2 Résumé

Cet article examine les effets de la structure forestière issue de pratiques divergentes d'aménagement du paysage sur les patrons spatio-temporels des épidémies de livrée des forêts (*Malacosoma disstria* Hubn.). L'objectif de cet étude était d'examiner l'association qui existe entre les patrons spatio-temporels des épidémies de livrée et 1) la configuration de la forêt, 2) la proportion d'espèces hôtes et 3) le climat. L'aire d'étude se situe à la frontière du Minnesota et de l'Ontario, où les frontières politiques ont créé un contraste entre l'héritage de l'aménagement: récolte à échelle fine au Minnesota, récolte à échelle grossière en Ontario, zone de conservation traversée par la frontière où peu d'aménagements récents ont été effectués. Les patrons spatio-temporels des épidémies de livrée des forêts ont été examinés en utilisant une reconstruction dendrochronologique à l'aide de peuplier (*Populus tremuloides*), l'hôte primaire de la livrée, échantillonné sur 14 sous-groupes à l'intérieur de l'aire d'étude. En utilisant des analyses de groupements pour série temporelle ainsi qu'une partition de la variance, les caractéristiques d'épidémies (périodicité, intensité, durée) ont été associé avec des données satellites de structure forestière et climatique. La partition de la variance à permis d'expliquer 36% de la variance dans les caractéristiques d'épidémies. Ces caractéristiques d'épidémies sont fortement associées avec la configuration forestière (32%) et celle-ci est aussi corrélée avec la proportion d'espèce hôtes. Les variables climatiques étaient associés avec la configuration (13% de la partition de la variance) mais avaient une valeur négative lorsque prisent indépendamment suggérant qu'à cette échelle, les effets de la structure forestière dominent. Nous avons aussi déterminé que les sous-groupes localisés dans la zone de conservation ont des épidémies désynchronisés en partie à cause d'une petite abondance d'espèce hôtes ainsi qu'une forêt plus continue dans cette zone. Nous suggérons que les forêts plus fragmentées où le peuplier faux-tremble domine, c'est-à-dire dans les paysages aménagés, pourrait expliquer les épidémies plus sévères et synchrones dans ces zones aménagées.

4.3 Introduction

Insect disturbance is a fundamental process that affects the ecological and economic systems of temperate and boreal forests. As one of the most important disturbance affecting more area than fire or harvesting (Dale *et al.*, 2001; Kneeshaw *et al.*, 2011), understanding insect disturbance is a concern for forest managers since insect damage can reduce timber volume, change landscape structure and affect nutrient cycling. Most damaging insects of the North American boreal forest are native (e.g., Mountain Pine Beetle (*Dendroctonus ponderosae* Hopkins), Spruce budworm (*Choristoneura fumiferana* Clem.) and Forest Tent Caterpillar (*Malacosoma disstria* Hubn.) and their historical outbreak dynamics have varied spatially and temporally (Cooke *et al.*, 2012; Gray *et al.*, 2000; Preisler *et al.*, 2012; Safranyik *et al.*, 2010; Simard *et al.*, 2002; Simard *et al.*, 2012). Although these variations may in part be influenced by climatic conditions they are also occurring at the same time as large-scale changes to forest landscape structure by forest management operations. These landscapes structure changes also depends upon policy in place and will differ between administrative regions or across international borders. This creates unplanned landscape-scale experiments that provide an opportunity to examine the interactions between climate, landscape heterogeneity created by forest management and their interaction with insect outbreaks dynamics.

Forest management practices can influence forest susceptibility to outbreaks by influencing landscape-scale abundance and connectivity of susceptible hosts (Carleton and MacLellan, 1994; Miller and Rusnock, 1993; Raffa *et al.*, 2008; Volney

et al., 1999). For example, it has been suggested that forest management activities have increased the proportion of host species and thus forest susceptibility to spruce budworm (Blais, 1983; Swetnam and Lynch, 1993). However, previous studies of the effects of management performed at the stand scale found little support for the notion that stand-level treatments by themselves influence defoliator dynamics but they provide evidence that forest composition affects damage severity (Muzika and Liebhold, 2000; Wesołowski and Rowiński, 2006). Similarly, studies performed at very broad regional scales often fail to capture landscape host pattern effects on outbreak dynamics since broad-scale patterns of macroclimate dominate outbreak temporal pattern (Cooke and Roland, 2000; Daniel and Myers, 1995; Fleming and Shoemaker, 1992; Roland *et al.*, 1998; Williams and Liebhold, 2000). In between the stand and regional level lies the landscape level, where forest managers have the capacity to influence spatial structure in terms of forest species composition and configuration. The effect of landscape-scale forest structure on insect outbreak dynamics has not been adequately quantified even though large changes in forest structure and composition have been documented (Candau *et al.*, 1998; Cyr *et al.*, 2009; Gray, 2013).

The forest tent caterpillar is an important native insect defoliator that causes considerable damage to hardwood species, particularly aspen, its primary host, as well as paper birch (*Betula papyrifera)* and sugar maple (*Acer saccharum*) (Witter and Kulman, 1979). Outbreaks, which have been occurring for centuries (Sippell, 1962), are synchronous over most parts of its range except in west central Canada and central Minnesota where they are asynchronous and lack periodicity (Hildahl and Reeks, 1960). In the boreal forest, forest tent caterpillar outbreaks generally last for 1 or 2 years with a recurrence interval of 6 to 16 years (Cooke *et al.*, 2012). Outbreaks

of the forest tent caterpillar are controlled by numerous mechanisms such as delayed density-dependent parasitism, of which the controlling parasitoids are themselves affected by climate and forest structure (Myers, 1998; Roland and Taylor, 1997). Forest heterogeneity and climate also influence the duration and extent of outbreaks (Cooke and Roland, 2000; Roland, 1993; Roland *et al.*, 1998). At the landscape scale, outbreaks can be disrupted by large-scale structural heterogeneity of host species leading to longer and more severe outbreaks in forests fragmented by agriculture (Roland, 1993; Roland and Taylor, 1997).

Past research in the Border Lakes region of Minnesota and adjacent Ontario has investigated the effects of divergent land management on forest spatial structure at multiple scales (James *et al.*, 2011a), and on spruce budworm dynamics (Robert *et al.*, 2012). Here we investigate the effect of this divergent land management on the spatio-temporal patterns of forest tent caterpillar outbreaks. In contrast with spruce budworm, the forest tent caterpillar has shorter return intervals which facilitates the reconstruction of outbreak history encompassing many outbreak cycles and thus, the evaluation of differences in temporal patterns. In this paper, our objective is to examine the degree of association between temporal characteristics of outbreaks (synchrony, periodicity and intensity) and forest landscape structure which include: host abundance, host age structure, and host configuration as well as climate variables.

4.4 Study area

The border lakes landscape is a 6 million ha ecoregion located at the international border between Minnesota (USA) and Ontario (Canada) (Fig. 4.1). Region-wide forest harvest activity started at the end of the 19th century and focused on selective harvest of the "big pines" (*Pinus strobus* L., *Pinus resinosa* Ait.) using waterways across the majority of the Border Lakes Landscape. Forest harvest patterns diverged between Minnesota and Ontario approximately 50 years ago, coinciding with mechanized clear-cutting operations on both sides of the border. In particular, clearcuts within managed Canadian forests were roughly an order of magnitude larger in size (Rempel *et al.*, 1997; Suffling *et al.*, 2003) than managed American forests to the south (harvest unit averaging 17 ha (Host and White, 2003)), though the landscape-scale rate of harvest was similar in both areas (James *et al.*, 2011a; Sturtevant *et al.*, 2014). Between these managed regions lies an approximately 1 million-ha wilderness area that includes Quetico Provincial Park in Ontario and the Boundary Waters Canoe Area Wilderness in Minnesota where no timber harvest has occurred since the early 1970s (Heinselman, 1996).

The study area lies within the transition zone between the Great Lakes-St. Lawrence mixedwood and boreal forest regions (Fig. 4.1). Its geomorphology is characteristic of the Canadian Shield, typified by a high density of lakes and wetlands (James *et al.*, 2011b; Superior Mixed Forest Ecoregional Planning, 2002). Forest composition within the ecoregion boundaries is best characterized as mixed "near boreal" (Heinselman, 1973) forest with a high proportion of boreal tree species (i.e.: jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), trembling aspen (*Populus tremuloides*), paper birch

(*Betula papyrifera), and* eastern larch (*Larix larcinia*), as well as tree species near their northern range(e.g., white pine (*Pinus strobus*), red pine (*Pinus resinosa*), and red maple (*Acer rubrum*)). Further north, composition becomes more boreal and conifer-dominated, whereas further south the composition becomes more temperate and deciduous-dominated (Sturtevant *et al.*, 2014). Studies conducted in the Boundary Waters Canoe Area concluded that, since 1910, decreasing fire frequency has changed the dominant pathway of succession from even-aged jack pine and aspen to an uneven-aged structure with a complex mixture of spruce, paper birch, and balsam fir (Frelich and Reich, 1995). In the absence of fire, other disturbances like wind, insects and senescence have become dominant (Mattson and Shriner, 2001). The managed part of the landscape contains similar forest types but has a higher dominance of early-successional forest classes due to forest management operations (Wolter and White, 2002).

4.5 Methods

4.5.1 Historical reconstruction of forest tent caterpillar outbreaks

We reconstructed the temporal patterns of forest tent caterpillar outbreak history using dendrochronological analysis of aspen tree cores sampled across north-south and east-west gradients in 57 sites (Fig. 4.1). Study sites were selected using a zonally stratified sampling design to account for variation in land management

legacies and dominant climatic gradients. Land management zones were defined as "fine" (fine-scale managed forests in Minnesota, labeled as "F"), "coarse" (coarse-scaled managed forests in Ontario, labeled as "C"), and "wilderness" (the wilderness area defined by the Boundary Waters Canoe Area and the Quetico Provincial Park labeled as "W") (Fig. 4.1). Sites within each land management zone were subdivided into 2 to 3 longitudinal groups of sites spanning the east-west extent of each zone. Longitudinal groups were further separated into northern and southern subgroups represented by a minimum of three sample sites with an average of 8 km between sites for a total of 14 subgroups. Throughout this article labels are thus identified using a management zone - longitudinal group - latitudinal subgroup terminology (Example: Coarse-Western-North or CWN). Longitudinal groups and latitudinal subgroups were defined to maintain similarity in the scale of area represented by each respective grouping.

Specific site locations were selected based on accessibility or, in the wilderness, along river corridors and lakeshores. Suitable stands were selected when 5-15 host canopy aspen trees were located. While sampling, we avoided stands located on high slopes or in low-elevation hydric areas. We sampled two cores at 1 meter height from at least 5 host trees per site that were 30 cm DBH or higher. Cores were stored in plastic straws and were later mounted, sanded (80, 150, 220, 400 grit size), and stained using Fehling solution (Asherin and Mata, 2001).

Tree-ring widths were measured using a Velmex uni-slide measuring table with an accuracy of 0.001 mm (Velmex Incorporated, Bloomfield, New York, USA). Tree chronologies were aggregated into their respective subgroups and we conducted a

site-level and subgroup-level crossdating analysis using COFECHA (Holmes, 1997) to locate missing or false rings, to test for measurement errors, and to eliminate problem series. Index chronologies were calculated using the program ARSTAN (Cook, 1985; Holmes, 1997) with a cubic smoothing spline to detrend the series and remove the age-related trend in growth (Cook, 1985). Spline parameters were set to a 50% frequency response cutoff of 50 years (Sutton and Tardif, 2007). From 18 to 42 trees were used to develop mean chronologies for each latitudinal subgroup. Table 4.1 provides summary statistics at the latitudinal subgroup level. We used a mean chronology in conjunction with soil moisture index data (SMI) (Hogg *et al.*, 2013) to assess and partial out the influence of drought on growth (Hogg *et al.*, 2002).

Dendrochronological reconstruction of outbreaks was done using the program OUTBREAK on aspen chronologies with a threshold growth reduction set to -1.28 standard deviations and a duration of 3 years (Sutton and Tardif, 2007). We did not correct the chronologies with non-host series such as those from white spruce (Sutton and Tardif, 2007) prior to introducing them to OUTBREAK to reduce the risk of introducing a noisy semi-periodic signal from other defoliator such as the spruce budworm (Bouchard *et al.*, 2006). OUTBREAK parameters used in this study have also been used successfully to reconstruct the outbreak history of forest tent caterpillar in other studies (Cooke and Roland, 2007).

Output from OUTBREAK was converted to frequency graphs to show the percentage of trees affected by each outbreak. We classified "outbreaks" as those time periods during which the number of trees showing growth reduction exceeded a defined threshold. Thresholds values varied from 20% to 50% to perform a sensitivity

analysis and to evaluate the degree to which interpretations were dependent on our definition of an outbreak (Robert *et al.*, 2012). These values (outbreak characteristics at different thresholds, Table 4.2) were used as response variables in further analysis.

Outbreak dynamics were characterized by recurrence interval, duration, and intensity (Table 4.2). Recurrence interval is the average interval between outbreaks which we measured as the mean time period between the first year of successive outbreaks (Blais, 1983). Intensity is often linked to population density and outbreak duration. For our study we used the highest percentage of affected trees for each outbreak as a proxy to evaluate intensity. We also evaluated duration as the number of years an outbreak occurred using the varying outbreak thresholds described above. Finally, we examined the spectral characteristics of the OUTBREAK time series using smoothed periodograms (Bloomfield, 2000). Spectral analysis was done using the "spec" function in R (R Core Team, 2008) and results tested against pink noise null periodograms (Chatfield, 2003) were then plotted and smoothed using Daniell smoothing strategies of 2 passes with half-width windows of 3 and 5 to minimize the spectral leakage of the data and to identify general areas of high spectral density (Bloomfield, 2000). The two highest significant spectra along with their cohesion levels were selected as the significant periods for each time-series.

4.5.2 Predictor variables

Climate

Climate in the study area varies with distance from Lake Superior (Sturtevant *et al.*, 2014), which can affect forest tent caterpillar dynamics (Cooke and Roland, 2000). Sites closer to the lake are more temperate than further sites which are more continental. Extreme cold or variable temperatures during overwintering can cause an outbreak to collapse over large areas (Blais *et al.*, 1955; Cooke and Roland, 2003) whereas cool springs are associated with population decline (Ives, 1973) and outbreaks that do not last long (Cooke and Roland, 2000). Aspen is also very sensitive to drought which, in addition to forest tent caterpillar defoliation, is implicated in aspen dieback (Hogg *et al.*, 2008).We therefore included historical climate in our outbreak pattern analysis. We extracted annual seasonalized temperature (winter, summer, spring) averages using minimum monthly averages of simulated temperature from an historical climate model (McKenney *et al.*, 2006) and we also included annual average simulated Soil Moisture Index (Hogg *et al.*, 2013; Swetnam and Lynch, 1993). These predictors where calculated for each subgroups and used in our statistical analysis of temporal pattern of forest tent caterpillar outbreak (see below).

Forest Structure

Relative basal area of aspen and forest age derived from a time-series of a land cover classifications was used as predictors variables in statistical analyses. Remotely-

sensed estimates of average aspen basal area from 2003-2004 (Wolter *et al.*, 2008) were calculated as an indicator of current host proportion. Forest proportion surrounding sample sites was quantified within a variable radius ranging from 0.5 to 50 km to assess the potential effect of different scales of measurement of this variable on the insect-host relationship (Table 3). We calculated average relative aspen basal area for each sample site and averaged it for each of the 14 subgroups. A similar methodology was used to extract age structure information from a time series (1975-2000) of remotely-sensed land cover classification based on LANDSAT imagery (Wolter *et al.*, 2012). Two age classes (post and pre 1975) were created for each subgroup and introduced as predictor variables in the statistical analyses. For forest configuration predictor variables, we included the mean patch size and the number of patches calculated through FRAGSTAT (McGarigal *et al.*, 2002) of Landsat classification map data (Wolter *et al.*, 2012) representing forested and open cover classes at a variable radius around each site (0.5 to 50 km; Table 4.3)

4.5.3 Statistical analysis

We visualized spatial patterns in temporal outbreak variation and the degree of similarity among subgroups using cluster analysis. If management legacies have an effect on outbreaks, one would expect to see clustering by management subgroup. We applied cluster analyses using both complete linkage and k-means methods with 3 centroids (since complete linkage clustering has shown that 3 main groups were present) where the output is plotted through a PCA using the "vegan" package in R

(Keogh and Kasetty, 2003; Oksanen *et al.*, 2013). Cluster analysis was applied to the percentage of affected trees to assess the similarity of time-series patterns using Euclidean distance as an index of similarity. Euclidean distance was used for its simplicity to implement and because it is widely used as a benchmark index in time-series analysis (Keogh and Kasetty, 2003).

Because we wanted to test the degree of synchronization between occurrences of outbreaks among managed zones, we examined spatial autocorrelation as a function of geographic distance using time-series of percent affected trees by management zone (Coarse, Fine, Wilderness). The Spatial Nonparametric Covariance Function (SNCF) found in the "ncf" R package (Bjørnstad and Falck, 2001) was used to complete this analysis. This analysis was performed at the site level (as opposed to the subgroup level in previous analysis) due to the low amount of possible pair-wise distance at the subgroup level. Since pair-wise distances between sites is much lower in the wilderness zone (maximum of 90 km), we scaled our analysis to this maximal distance. Furthermore we bootstrapped our SNCF by resampling our sites within an equivalent area of the wilderness zone which contained a minimum of 5 sites. The SNCF was calculated within these subsamples and an average with 95% CI is provided to test the significance of our SNCF analysis performed at the management zone level.

Next, we evaluated the relative influence of predictor variables (i.e., management zone, climate, and current forest conditions) on outbreak characteristics using selected predictors for each category in a variance partitioning analysis (Borcard *et al.*, 1992). Potential predictors representing current forest conditions were the average

percentage of host trees as well as the percentage of forests that are older than 1975 stand origin, each assessed at several scales (0.5 km to 50 km radius) around each site. Potential predictors representing climate drivers included seasonal minimum mean temperature for spring, summer, and winter as well as Soil Moisture Index (SMI) index for each subgroup (Table 4.3). Due to the high total number of predictors (15 total), we used forward selection on the full set of predictor variables to identify a significant subset using the R package "packfor" (Dray, 2011) prior to the variance partitioning analysis. The high number of response variables present in the outbreak characteristics dataset did not allow for a forward selection protocol to give statistically valid results, thus we applied forward selection using the annual percentage of affected trees as the response variable. We compared the forward selection results with separate ANOVA and linear regression analyses to ensure potentially important predictors were not missed by the selection process.

Variance partitioning of the RDA solution was undertaken using the Varpart function in the Vegan package in R (Legendre *et al.*, 1998; Oksanen *et al.*, 2013). In this variance partitioning, the response matrix was a scaled table of outbreak characteristics and a set of predictors reflecting each hypothesis (see tables 4.2 and 4.3). The response dataset included the two highest peak frequencies (converted to period) from spectral analysis, their spectral density, and outbreak characteristics (i.e., number of outbreaks, intensity, and recurrence interval). All these outbreak characteristics were calculated in our sensitivity analysis of outbreak threshold, using outbreak threshold values of 20%-25%-30%-50% trees affected (Table 4.2). Variance partitioning allowed us to examine the unique contribution of each group of predictors selected by the forward selection process and to assess the degree of support for our hypothesized drivers affecting forest tent caterpillar outbreaks in

different regions of the Border Lakes Landscape. The adjusted R square was used to assess the proportion of variance associated with each partition (Peres-Neto *et al.*, 2006).

4.6 Results

4.6.1 Outbreak summary and groupings in the landscape

We outlined differences between major outbreaks events, i.e., those that surpass the highest threshold 50% affected trees, and minor defoliations that only surpass the lower threshold 20% affected (Table 4.2). When considering an outbreak threshold of 20% or 25% affected trees, we identified 4 to 7 outbreaks for each subgroup with a return interval that varied between 12 and 33 years (Table 4.2). The highest return intervals were found in the wilderness zone although subgroups such as the Fine Western South and Coarse Eastern South also showed return intervals above 20 years at the 25 % threshold. Recurrence intervals of higher intensity outbreaks (i.e, 30% to 50% affected trees) varied from 12 to 62 years. The higher return intervals were mostly indicative of very-high intensity outbreaks with a few low-intensity outbreaks such as those found in the Fine Eastern North or the Wilderness East South subgroup. Spectral analysis of the percentage of trees affected also confirmed this pattern of variable intensity outbreaks within individual subgroups and showed periodicity that fluctuated from 9 to 31 years (Table 4.2). Subgroups with periods longer than 20 years were the Fine Center North subgroup and the Wilderness Eastern South

subgroup. Thus, there is variation in outbreak pattern within subgroups, perhaps due to variations in the presence of host species in some locations (e.g., Wilderness East North), which creates a changing pattern of frequent-low intensity outbreak to infrequent-high intensity outbreaks (Fig. 4.2)

Cluster analysis revealed the presence of three major groupings of outbreaks in the landscape (Fig. 4.2 and 4.3). The first cluster was composed of Fine Eastern and Fine Center subgroups which can be characterized by outbreaks that are slightly more frequent than elsewhere (Table 4.2). The second cluster includes subgroups from the Wilderness Western North, Wilderness Eastern North, Fine West North, and the Coarse Eastern subgroups. The last cluster contains a mixture of subgroups mostly located in the west, including the Wilderness Western South, Wilderness Eastern South, Coarse Western subgroups, and Fine Western South subgroups. Despite some exceptions, the clustering seems to indicate an east-west gradient or a gradient of distances from Lake Superior. Clustering by management zone is not obvious, with the important exceptions of the Fine Central group and the Fine East group

4.6.2 Subgroup synchrony

The SNCF is a measure of spatial covariance amongst pairs of time-series. Its purpose is to estimate the distances over which fluctuations in two time-series are synchronized. All zones showed decreasing correlation with distance but the

wilderness zone has a lower correlation than the global mean SNCF, the fine zone and the coarse zone (Fig. 4.4). Both the fine and the coarse zone had a higher correlation suggesting that outbreak where more synchronized than the global mean. Both these zones also had a higher correlation then our bootstrapped estimate of SNCF which indicate that the correlation is different from random samples of sites taken at similar distance. In opposition the SNCF of the wilderness subzone is lower than our bootstrapped estimate of SNCF suggesting that outbreaks within this zone are less synchronized than a random sample of sites. This is also consistent with our cluster analysis where wilderness subzones tend to group with adjacent subgroups then between themselves. Importantly, subgroups from the wilderness zone also had lower proportion of aspen, higher proportion of non-host species and more continuous forest than managed areas (Fig. 4.5).

4.6.3 Climate, forest configuration or proportion?

Predictors selected through the stepwise selection protocol for forest configuration, forest proportion and climate datasets were: 1) For forest configuration: the Number of upland forest patches at 5 km scale, Number of upland grass patches at 40 km scale, and the mean patch size of upland grass class at 0.5 km scale; 2) For forest proportion variables: the percent basal area of host trees within 0.5km, 20km and 50km radius of each site 3) For climate variables: spring minimum temperature and winter minimum mean temperature. The final RDA model resulted in 36% of the total variance being explained by all predictors (Fig. 4.6). Climate variables by themselves

had a negative value for variance explained but the interaction between forest configuration and climate variables amounted to 13% of variance explained. Forest configuration variables by themselves had the highest amount of variance explained with a value of 34% and is the largest value. Forest proportion variables had a low amount of variance explained with 3% and are correlated with forest configuration variables since their interaction also had a negative value. The apparent additive discrepancies between total variance explained and its separation among hypotheses comes from the shared proportion of variance explained which is often negative. The various values of variance explained shows that forest configuration variables dominated the variance partitioning but negative and high intersection value between forest configuration and forest proportion/climate shows that hypothesized drivers were not mutually exclusive.

4.7 Discussion

We evaluated the effect of three groups of variables (forest configuration, forest proportion, and climate) on forest tent caterpillar outbreak characteristics: synchrony, periodicity and intensity. We hypothesized that forest management, through its effect on forest structure such as an increase in aspen proportion and modification of landscape connectivity, would influence these outbreak characteristics (Robert *et al.*, 2012; Roland *et al.*, 1998). Although the 3 datasets used in this study represent hypotheses that are not mutually exclusive, the effect of configuration (34% of variance explained) dominated the variance partitioning suggesting that values of

configuration have a predominant effect on the variation of forest tent caterpillar outbreak characteristics.

Management has a direct effect on forest structure (configuration, age class and composition) as younger post-harvest stands have a much higher proportion of forest tent caterpillar host species than older forests (Carleton and MacLellan, 1994; Wolter and White, 2002). Furthermore, evidence exists that early-successional stands usually dominated by jack pine are being replaced with aspen stands following harvest (Frelich and Reich, 1995). In our study, the basal area of aspen increased in both managed zones in comparison to the wilderness zone where more forests are in advanced successional stages (James *et al.*, 2007; Sturtevant *et al.*, 2014; Wolter *et al.*, 2008). The mechanism for the effect of forest structure on outbreak characteristics may in part be explained by forest configuration and its influence on parasitoids of the forest tent caterpillar which allow outbreak to develop more rapidly in fragmented landscape (Roland, 2005). Roland and Taylor (1997) have also shown that for four known forest tent caterpillar parasitoids, host densities affected parasitoid movement (Roth *et al.*, 2006). It could also be explained by lower rates of dispersal losses in continuous forests and thus higher rates of inter-population migration which promote cycle synchronization (Barbour, 1990).

Although the current forest structure (proportion and configuration) datasets represents is only a snapshot of current conditions, we suggest that current forest structure is representative of past forest composition. This conjecture is consistent with the insect response reflected in the variance partitioning where forest configuration explain most of the variation. The analysis of outbreak characteristics

outlines important differences between subgroups located in the wilderness zone versus outbreaks located in the managed zones. Considering that wilderness subgroups contained more continuous forest and a lower amount of aspen compared to managed forests, it is possible that outbreaks in the wilderness zone were supplemented by forest tent caterpillar populations immigrating from outside the wilderness zone. This is supported by our SNCF analysis which identified lower correlation within the wilderness area in comparison to other areas (Fig. 4.4) but also by the cluster analysis (Fig 4.3) which outlined an east-west gradient that is not related to climate as shown by the partition of variation (Fig 4.6). Forest tent caterpillar populations from the aspen-dominated managed zones may thus act as source population which leads to synchrony between wilderness subgroups (sink population with low emigration) (Dunning *et al.*, 1992) and outbreaks in adjacent managed zone subgroups (Cooke *et al.*, 2012). In other words, the low proportion of host species in the wilderness zone may not provide the necessary degree of host connectivity to facilitate within-zone cycle synchronization via inter-population migration. The lower covariance of the SNCF function in the wilderness supports this interpretation, in that it shows that populations are more synchronous between zones than within. Dispersal by adults (Johnson *et al.*, 2004) has been proposed as an important mechanism at stand and regional scales for the synchronization of insect outbreaks by linking spatially disjunct populations (Barbour, 1990). Given that forest structure is thought to affect insect dispersal rates in this system (Roland and Taylor, 1997), this supports the idea that fragmented forest with higher proportion of aspen are more prone to short, but synchronous, high-amplitude cycles in defoliator numbers, as suggested by Cooke *et al.* (2012).

The variability in outbreak frequency at individual sites may be linked to changing

proportions of host species as suggested by Cooke and Lorenzetti, (2006). Although Roland (1993) did not detect an effect of host proportion, it is likely that the effect of host proportion occurs at smaller scales than the one described in his study (Roland and Taylor, 1997). Considering that forest harvesting increases the proportion of aspen in cut-blocks (Carleton and MacLellan, 1994) and that aspen content decreases with time since stand initiating disturbance (Bergeron, 2000), fluctuations in the proportion of aspen could have a direct influence on the occurrence of outbreaks, and thus may explain the variability in outbreak frequency that occurs at any given site through time.

Forest tent caterpillar is known to be sensitive to climate as is its host species (aspen), and part of the response observed in the analysis of outbreak characteristics could be explained by errors on the dendrochronological reconstruction or by differences in climate between subgroups (Hogg, 1999; Hogg *et al.*, 2002). Concerning the dendrochronological reconstruction, aspen growth is reduced during drought conditions (Hogg *et al.*, 2013), which could lead to the detection of false outbreaks in the tree-ring records. However, like Cooke *et al.* (2007), we did not observe any relationships between drought and growth reductions in aspen chronologies or with outbreak characteristics during forward selection.

Differences in climate between subgroups may however account for the influence of climate variables within our variation partitioning (high intersection value with forest configuration). Population dynamics may be influenced by the East-West gradient in climate variables since warmer summer temperatures and lower precipitation as well as cooler winters and warmer springs were observed in the west; possibly due to the

warming (maritime) effect of Lake Superior (Sturtevant *et al.*, 2014). The east-west pattern revealed by the cluster analysis is also suggestive of a climatic influence on forest tent caterpillar outbreak dynamics at the scale of our study. Cooke et Roland (2003) noted that cold winters and warm springs are correlated with the onset of outbreaks whereas cool springs are associated with population decline and act to desynchronize caterpillar and host tree development (Cooke and Roland, 2003). However the variance partitioning of the RDA indicates this climatic effect is subtle relative to drivers associated with forest management legacy – particularly as they affect configuration of forested landscape.

4.8 Conclusion

The diversity-stability hypothesis predicts that the presence of one or a few specific species, rather than overall diversity, is the determinant of stability against disturbances (Ives and Carpenter, 2007). Unfortunately, the influence of tree composition on insect herbivory is usually difficult to assess due to the confounding effects of factors such as site conditions, climate, and forest composition/configuration on the insect and its host (Koricheva *et al.*, 2006). This study takes advantage of a natural landscape-scale experiment where we can independently observe the effect of landscape structure on insect outbreaks and offers an alternative to broad-scale manipulative experiments. At the spatial scale of our study and using a time-series based approach, we suggest that management has modified the landscape and influenced the host configuration and composition of the

landscape. The change in host pattern among the management zones may have desynchronized forest tent caterpillar outbreaks between managed and wilderness zone (Cooke and Lorenzetti, 2006; Cooke *et al.*, 2012). Thus it is likely that management, by changing forest pattern will also modify forest tent caterpillar outbreak characteristics. The implication of this research is that land management may have unintentional consequences on ecological processes occurring at the landscape level.

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4.11 Tables and Figures

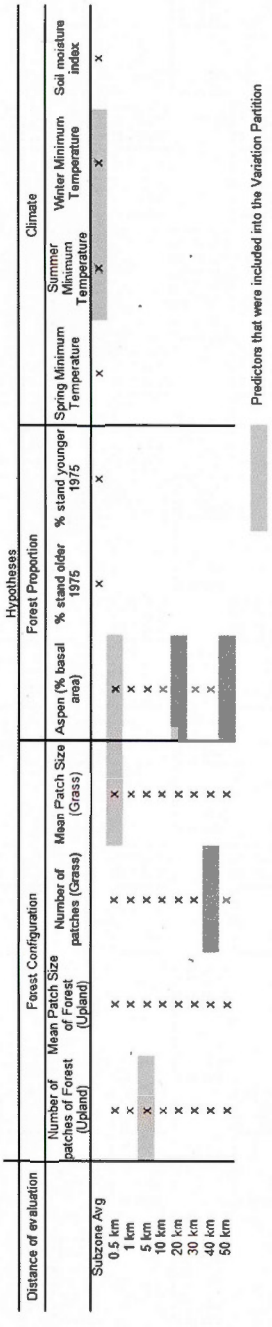
Table 4.1 : COFECHA output of summary statistics (mean ring width, sensitivity and inter-tree correlation) of the dendrochronological reconstruction for all subgroups.

							Sensitivity		
Zone	Group	Subgroup	Idtag	No. of trees	Time Span	Mean Ring Width (mm)	Mean	SD	Intertree Correlation
Coarse	Eastern	North	CEN	23	1887-2006	1.58	0.28	0.652	0.368
Coarse	Eastern	South	CES	30	1908-2006	2.19	0.274	0.844	0.354
Coarse	Western	North	CWN	31	1932-2006	1.84	0.37	0.884	0.453
Coarse	Western	South	CWS	23	1898-2006	1.79	0.335	0.793	0.385
Wilderness	Eastern	North	WEN	21	1904-2006	1.71	0.345	0.776	0.517
Wilderness	Eastern	South	WES	22	1880-2006	1.56	0.324	0.677	0.372
Wilderness	Western	North	WWN	25	1899-2006	2.13	0.336	0.964	0.494
Wilderness	Western	South	WWS	20	1903-2006	1.77	0.358	0.83	0.505
Fine	Center	North	FCN	26	1919-2006	1.87	0.307	0.863	0.358
Fine	Center	South	FCS	33	1919-2006	2.1	0.327	0.976	0.481
Fine	Eastern	North	FEN	24	1891-2006	1.43	0.295	0.693	0.451
Fine	Eastern	South	FES	18	1925-2006	2.21	0.27	1.032	0.471
Fine	Western	North	FWN	42	1927-2006	2.01	0.316	0.84	0.599
Fine	Western	South	FWS	30	1924-2006	2.15	0.291	0.934	0.454

Table 4.2 : Changes in the number of outbreaks, their duration, their recurrence and their intensity across landscapes with different land-use based on different threshold criteria for the determination of outbreaks (20, 25, 30 and 50%).

Zone	Group	Subgroup	Idtag	No. of Outbreaks				Average Duration (years)				Average Intensity (Max percentage of trees affected)				Recurrence Interval				Period (1st peak)	Period (2nd peak)	Spectral Density (1st peak)	Spectral Density (2nd peak)
				20%	25%	30%	50%	20%	25%	30%	50%	20%	25%	30%	50%	20%	25%	30%	50%				
Coarse	Eastern	North	CEN	7	6	3	2	4	3	4	3	35	44	61	72	13	19	28	16	15	9	1890	527
Coarse	Eastern	South	CES	7	4	4	3	4	5	5	2	40	46	53	58	18	23	23	10	18	6	1089	281
Coarse	Western	North	CWN	5	4	4	1	4	4	4	3	46	53	53	81	16	16	16	0	11	5	1197	247
Coarse	Western	South	CWS	6	6	5	3	4	4	3	1	45	45	49	56	15	15	16	32	14	6	1511	241
Wilderness	Eastern	North	WEN	6	4	4	4	4	4	4	3	45	68	68	68	15	22	22	22	15	8	2527	733
Wilderness	Eastern	South	WES	4	4	3	3	4	4	4	3	63	63	75	75	16	33	45	45	31	8	1463	508
Wilderness	Western	North	WWN	7	5	5	4	4	4	3	2	40	47	48	52	18	17	14	19	17	3	1516	42
Wilderness	Western	South	WWS	7	6	4	4	4	4	4	2	35	51	64	64	13	18	21	21	14	8	2180	617
Fine	Center	North	FCN	4	4	3	2	5	4	3	3	49	49	56	65	16	16	22	23	23	6	1465	129
Fine	Center	South	FCS	6	5	5	2	4	4	4	4	51	57	57	80	14	12	12	22	9	6	1978	241
Fine	Eastern	North	FEN	5	6	3	2	4	3	4	4	49	49	63	72	23	17	32	62	17	7	1399	388
Fine	Eastern	South	FES	7	6	4	2	4	3	3	3	39	42	50	67	12	12	19	15	16	7	1712	410
Fine	Western	North	FWN	5	5	4	2	3	3	3	4	51	51	57	76	18	18	22	37	16	6	1677	371
Fine	Western	South	FWS	5	4	4	4	4	4	3	2	48	55	55	57	19	21	21	22	14	6	974	259

Table 4.3 : Table containing available predictors for each of our hypotheses and their distance from each dendrochronological sites at which they were evaluated.



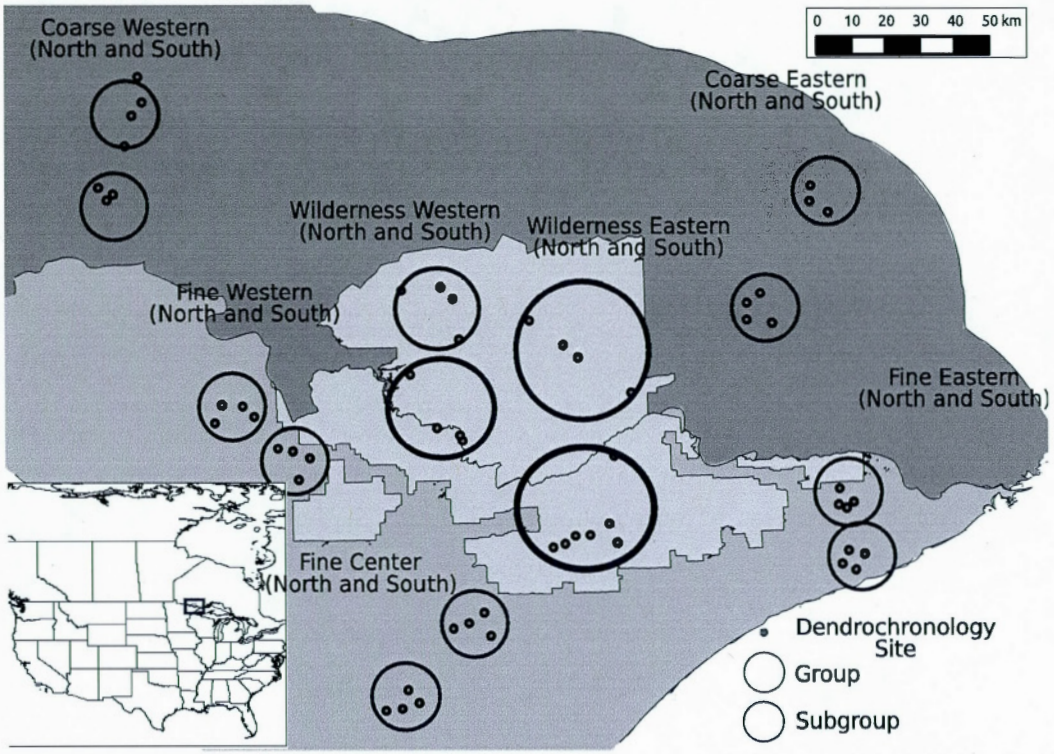


Figure 4.1 : The Border lakes landscape study area located at the border between Ontario (Canada) and Minnesota (United States). Points represent sampling sites for dendrochronological reconstructions of outbreaks.

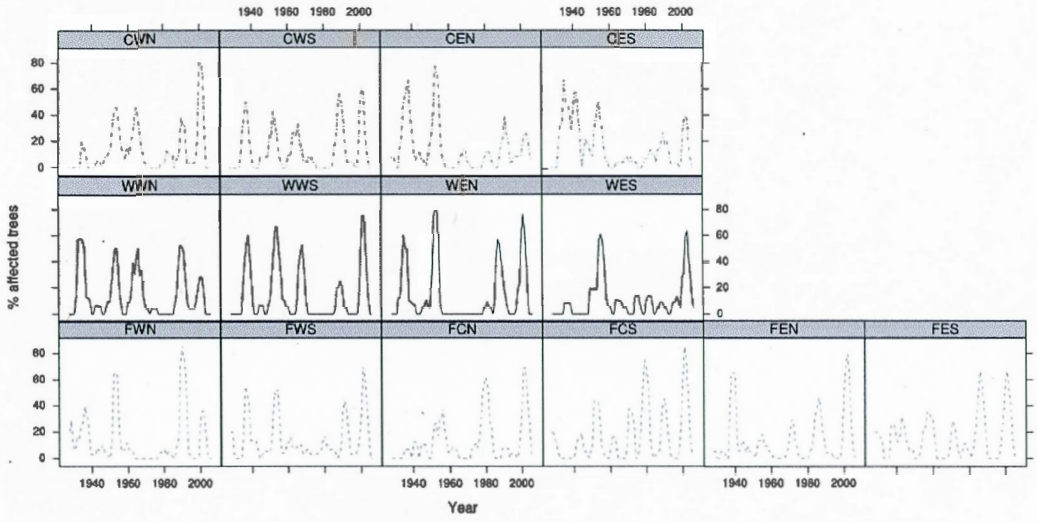


Figure 4.2 : Frequency graph of the program OUTBREAK showing percentage of affected trees throughout time for each subgroups:Wilderness (Black), Coarse-grained (Gray) and Fine-grained (Gray)

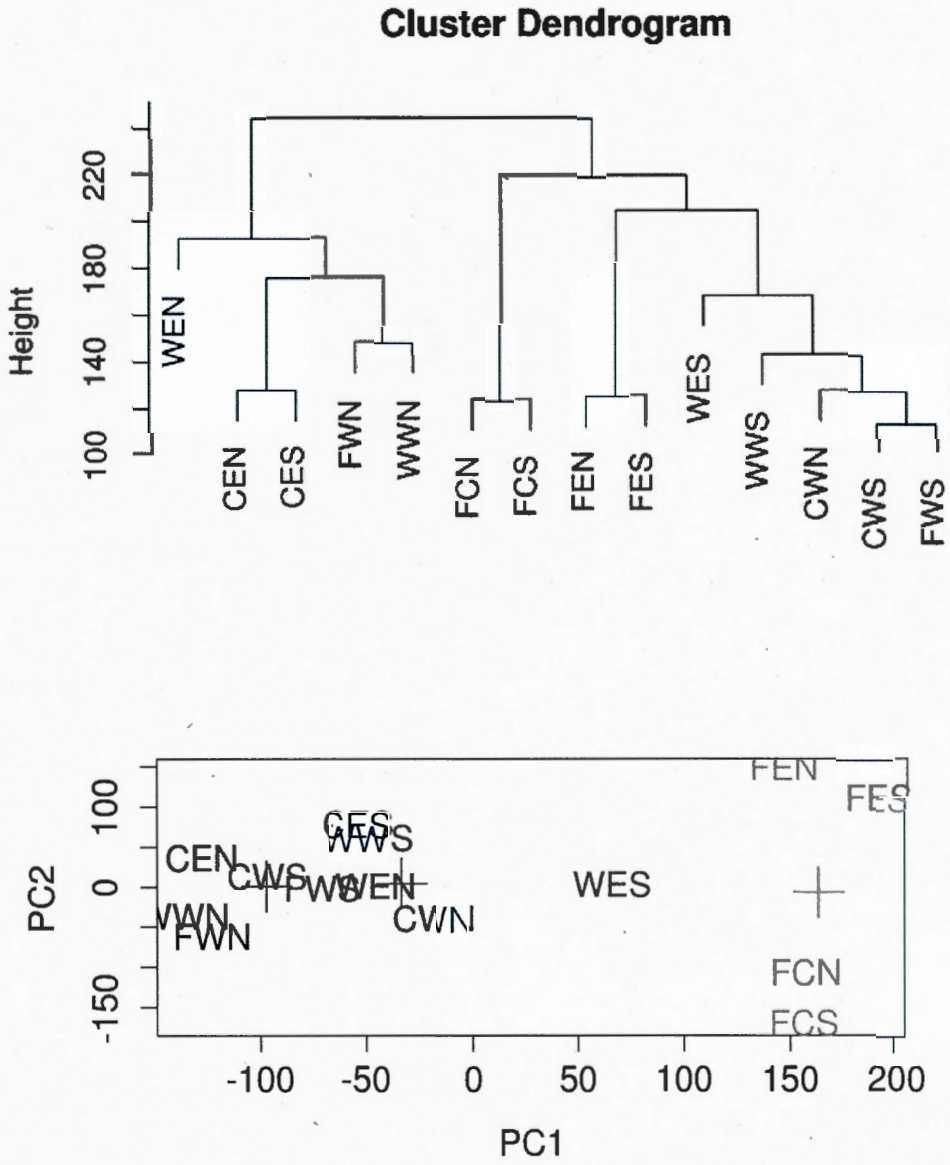


Figure 4.3 : Temporal cluster analysis and PCA representation of k-means cluster analysis using 3 centroids.

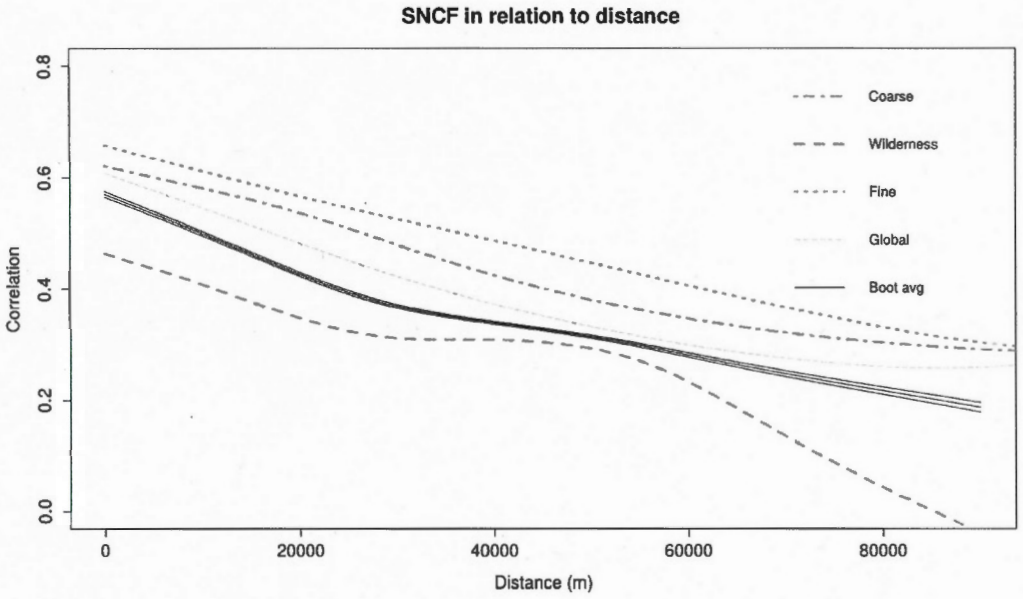


Figure 4.4 : Spatial non parametric covariance function for each of our management zone (gray, wide lines) with whole landscape value (gray, small line) and average bootstrap estimate with 95% CI (black)

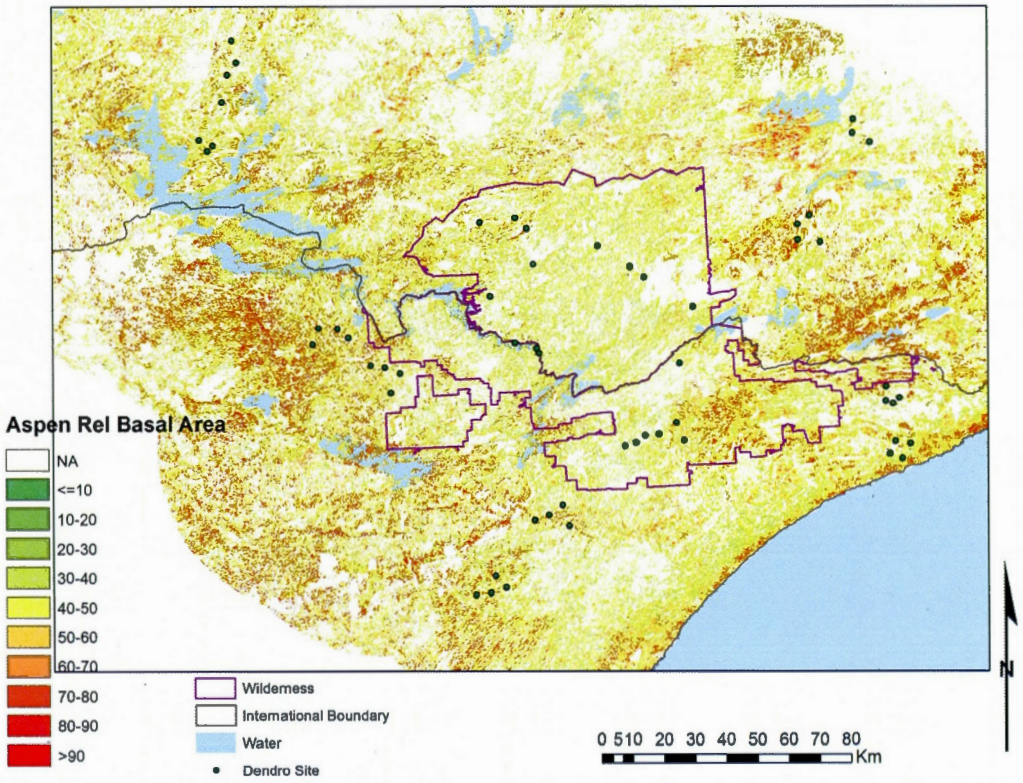


Figure 4.5 : Relative aspen basal area over the study area. Points represent dendrochronology sites.

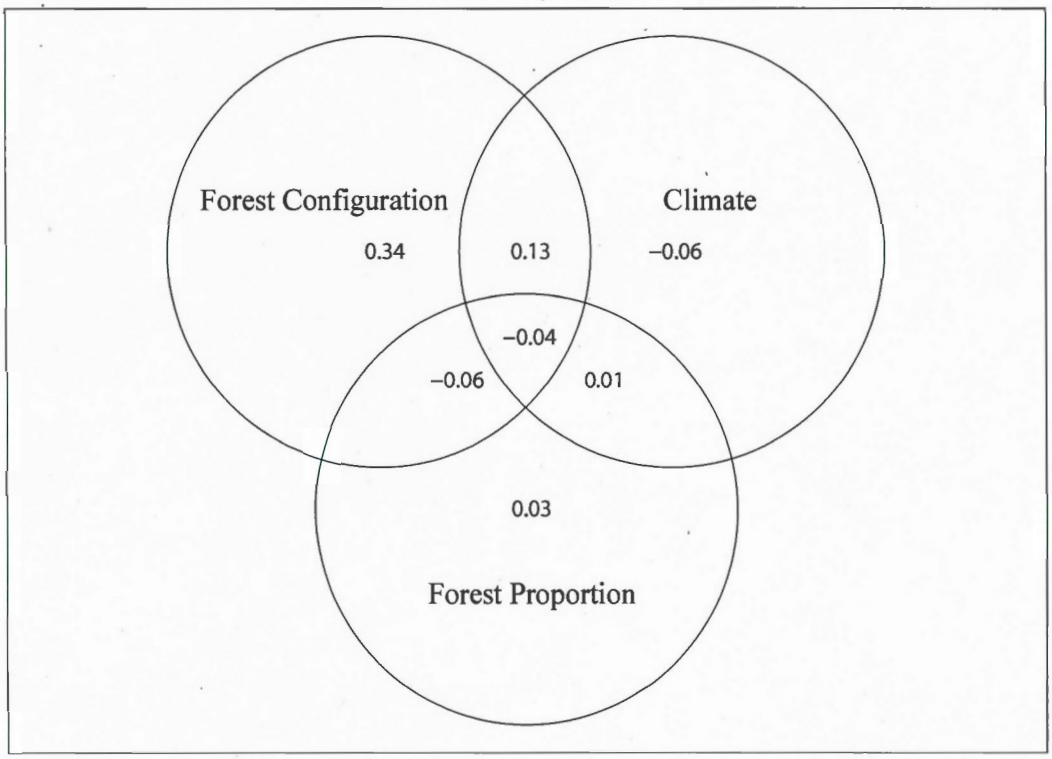


Figure 4.6 : Variation partitioning using predictors chosen by forward selection for each of our 3 hypotheses (Forest configuration, Forest proportion and Climate) using outbreak characteristics as response variable.

CONCLUSION GÉNÉRALE

L'influence des activités anthropiques sur les perturbations naturelles est devenue une importante préoccupation due au risque accru de changements environnementaux indésirables ou de perturbation à grande échelle (Dale *et al.*, 2001). Comprendre l'historique des perturbations ainsi que les facteurs influençant leurs variabilités peut permettre d'anticiper leurs impacts. Dans l'ensemble de cette thèse, nous avons examiné plusieurs facteurs pouvant affecter la dynamique spatio-temporelle des épidémies d'insectes. Malgré le fait que ces facteurs soient souvent difficiles à examiner indépendamment à l'échelle de notre étude, nous avons démontré que les modifications de la structure forestière suite à l'aménagement forestier ont engendré des modifications de la dynamique des épidémies d'insectes. Ainsi, nous présentons plusieurs avancées permettant une meilleure compréhension de la dynamique des épidémies d'insectes en milieux forestiers ainsi que sur l'influence des changements provoqués par l'aménagement forestier à l'échelle du paysage sur leur dynamique. Cette section relate l'ensemble des contributions de cette thèse pour ensuite nous transporter sur les possibilités de future recherche découlant de celle-ci.

En utilisant une approche dendrochronologique, nous avons reconstitué les épidémies de 2 espèces d'insectes, soit la tordeuse des bourgeons de l'épinette ainsi que la livrée des forêts, et ce, à l'intérieur d'une même zone de recherche. Cette zone de recherche située à la frontière du Minnesota et de l'Ontario à la particularité d'avoir été soumise à des régimes forestiers différents (c.-à-d. aménagement fin versus aménagement grossier) et d'être situé autour d'une zone de conservation traversant la frontière canado-américaine. Cette zone définit donc une expérience naturelle par laquelle il est possible de comparer une dynamique « naturelle » des épidémies d'insectes situées

dans la zone de conservation avec celle se situant dans les zones aménagées. Cette recherche est, à notre connaissance, la première tentant de quantifier les effets des legs créés par l'aménagement forestier sur la dynamique spatio-temporelle des épidémies d'insectes à l'échelle du paysage.

Notre premier chapitre tente de déterminer s'il est possible d'observer des différences dans les cycles temporels des épidémies à l'échelle du paysage en fonction des legs forestiers laissés par l'aménagement. Pour ce faire, nous avons examiné les épidémies d'un insecte à grande capacité de dispersion, soit la tordeuse de bourgeons de l'épinette. Grâce à notre design expérimental, nous avons démontré, dans le contexte de cette expérience naturelle, qu'il existe des différences dans la dynamique des épidémies entre les zones d'aménagement forestier et que ces différences sont difficilement explicables par la variabilité climatique entre les sites. Ainsi, nous avons conclu que les legs forestiers laissés par un aménagement plus fin désynchronisent les épidémies et réduisent leur intensité comparativement à la zone de conservation. Un aménagement favorisant des blocs de coupes plus grossiers, quant à lui, suggère que les caractéristiques décrivant les épidémies sont un mélange de la zone de conservation et de la zone d'aménagement fin.

Notre second chapitre tente de déterminer s'il est possible de discerner l'influence de plusieurs covariables sur les patrons temporels des épidémies de tordeuse de bourgeons de l'épinette parmi les trois zones d'aménagements forestiers. Le deuxième chapitre contient aussi un test plus explicite du degré d'association entre la tordeuse des bourgeons de l'épinette et des covariables reliées au climat ainsi qu'aux conditions forestières courantes. À travers une partition de la variance, nous avons démontré que

nos variables explicatives permettaient d'expliquer 35% de la variance totale distribuée entre les variables de configuration (14%), la proportion forestière (12%) ainsi que le climat (0.2%). Une analyse de groupement a démontré la dominance de l'effet des zones d'aménagement sur les patrons spatio-temporels des épidémies de tordeuse. À l'échelle de notre étude, nous suggérons donc que malgré une influence climatique, les modifications du paysage affectant la proportion et la configuration des espèces hôtes ont modifié les patrons temporels des épidémies de tordeuse. De plus, notre étude appuie les conclusions d'une étude à grande échelle faite au Québec qui suggère que la variabilité observée dans les patrons des épidémies à différents endroits devrait être interprétée comme des variations sur un patron de fond (Jardon *et al.*, 2003).

Parmi les causes pouvant expliquer ces résultats, les preuves scientifiques pointent vers l'effet cumulatif des changements de la composition forestière résultant des activités anthropiques. Plusieurs ont conclu que la fréquence et la sévérité des épidémies de tordeuse ont augmenté durant le 20e siècle (Blais, 1983; Swetnam and Lynch, 1993) (l'hypothèse sylvicole) tandis que d'autres auteurs comme Boulanger *et al.* (2012) démontrent que la fréquence des épidémies est stable depuis les 400 dernières années. Les études démontrant un effet de l'aménagement ont souvent fait des corrélations avec les changements des caractéristiques des épidémies dans le temps et l'augmentation de l'étendue de la foresterie. La résolution du débat sur l'influence de l'aménagement forestier à grande échelle sur les épidémies de tordeuse était, jusqu'à présent considéré comme étant impossible à cause de l'étendue à laquelle des manipulations doivent être exécuté pour mener à terme une expérience qui testerait l'effet de l'aménagement (Miller and Rusnock, 1993). Malgré cette lacune, plusieurs études ont mis en relation la sévérité ou la mortalité due aux

épidémies avec la composition arborescente des peuplements (Bergeron *et al.*, 1995; MacLean, 1980; Su *et al.*, 1996). Cependant, des résultats contradictoires sur l'effet de mosaïque forestière sur les épidémies ont aussi été observés, mais ceux-ci semblent dépendre de l'échelle d'observation (Bergeron *et al.*, 1995; Campbell *et al.*, 2006; MacKinnon and MacLean, 2004). Notre étude s'inscrit dans ce courant; l'utilisation d'une approche favorisant une expérience naturelle à grande échelle nous a permis d'évaluer plus directement l'effet de l'aménagement et les influences de la structure du paysage sur la dynamique temporelle des épidémies d'insectes. Nous appuyons, donc en partie l'hypothèse sylvicole, car nos données démontrent un effet de la structure du paysage (proportion et configuration) sur la dynamique des épidémies. Par contre, nos résultats sont contraires à ceux de Blais (1983) quant à l'augmentation de la sévérité due à l'aménagement forestier. Nous démontrons que pour plusieurs endroits, les épidémies sont stables, mais qu'un aménagement plus intensif pourrait réduire la sévérité des épidémies de tordeuse, une conclusion aussi appuyée par James *et al.* (2011). Des épidémies moins sévères pourraient aussi dire qu'il serait plus facile de gérer le rendement, car malgré le fait qu'elles soient toujours présentes, elles seraient de plus faible sévérité et moins étendues.

Considérant l'influence possible de l'aménagement sur les épidémies de tordeuse des bourgeons de l'épinette, nous avons tenté de déterminer si ces résultats se maintenaient lorsqu'appliqués à une autre espèce d'insecte (1) possédant une plus faible capacité de dispersion (2) ayant des cycles épidémiques plus fréquents (cycles deux fois plus courts que ceux de la tordeuse) et (3) s'attaquant à un hôte différent de la tordeuse. Cette approche qui consiste à tester les effets de la structure du paysage sur deux espèces d'insectes se contrastant, et ce, sur un même territoire est aussi unique dans la littérature. Le chapitre 3 a donc été effectué dans la même aire d'étude

que les deux chapitres précédents, mais porte plutôt sur une reconstitution des épidémies de la livrée des forêts. De la même façon, nous avons effectué une analyse du degré d'association entre diverses caractéristiques des épidémies et des facteurs explicatifs (i.e : configuration forestière, facteurs associés à la proportion d'espèces hôtes ainsi que des facteurs reliés au climat). Nos résultats démontrent que la configuration du paysage explique 34% de la variation (sur un total de 36%) et qu'il existe aussi une forte relation avec la configuration et le climat qui explique 13% de la variation. Nos données démontrent aussi que le peuplier faux-tremble, une espèce qui s'installe après perturbation, a augmenté en proportion avec l'accroissement de l'aménagement forestier dans les zones aménagées en comparaison avec la zone de conservation où les résineux, typiques de la fin de succession, dominent le paysage (Bergeron, 2000). Un corollaire est que l'ensemble des sous-groupes localisés dans la zone de conservation ont une plus faible abondance de l'espèce hôte de la livrée, ce qui contribue à désynchroniser les épidémies localisées dans cette zone. Ceci expliquerait le fait que les sous-groupes de la zone de conservation soient plus synchronisés avec les sous-groupes des zones aménagées adjacentes plutôt qu'avec les sous-groupes situés à l'intérieur de la zone de conservation.

Les épidémies de la livrée des forêts sont généralement cycliques pour l'ensemble de la province de l'Ontario (Hildahl and Reeks, 1960), mais peuvent varier pour d'autres régions de la forêt boréale. En 2006, Cooke et Lorenzetti ont décrit des variabilités régionales de l'intervalle de retour notamment pour l'Abitibi et la région Appalachienne du Québec. Ceci leur a permis de conclure que malgré le fait que les cycles de la livrée des forêts étaient réguliers, il existait des régions où les densités de population n'étaient pas assez élevées pour causer des dommages détectables (Cooke and Roland, 2007) créant ainsi de la variabilité dans les patrons d'épidémies. Cette

variabilité dans les cycles de la livrée est aussi présente dans notre chapitre 3, où nous avons observé que les épidémies de la livrée se propagent des zones aménagées vers la zone de conservation. Ceci pourrait aussi expliquer le fait que certaines zones ne sont pas soumises à des épidémies ou n'ont carrément pas d'épidémie détectable (c.-à-d. : la zone de conservation). Plusieurs facteurs sont suspectés de moduler l'amplitude et le cycle de la livrée, par exemple, la composition forestière pourrait jouer un rôle dans la dispersion de l'insecte (Roland and Taylor, 1997). Cela supporte l'idée qu'une forêt continue en espèces hôtes serait plus encline à des épidémies courtes, mais synchrones et de haute amplitude comme suggérée par Cooke *et al.* (2012). Ce constat est aussi similaire pour les épidémies de la tordeuse des bourgeons de l'épinette, qui ont été plus sévères et synchrones dans les zones de forêts où le patron des hôtes est plus continu que dans les paysages hautement fragmentés où les épidémies de la tordeuse ont été désynchronisées. Dans le cas de la livrée, l'aménagement forestier peut être une source de changement de proportion du peuplier faux-tremble, car c'est une espèce qui apparaît fréquemment dans les parterres de coupes (Carleton and MacLellan, 1994). Nous n'avons pas observé des différences entre les deux types de forêts coupées (petites coupes dispersées vs grandes coupes agrégées), mais notre étude permet d'observer un effet de l'aménagement forestier sur les caractéristiques des épidémies qui est lié à l'enfeuillement des territoires aménagés.

Cette thèse fournit donc plusieurs constats sur l'influence des legs créés par l'aménagement forestier à l'échelle du paysage. La force de cette thèse est de démontrer que les activités humaines à grande échelle ont un effet sur les patrons temporels d'épidémies. Par exemple, les cycles de tordeuse sont plus fréquents, mais moins sévères dans les zones d'aménagement plus intensives. Ceci suggère qu'un

aménagement plus fin pourrait promouvoir ce type d'épidémie. La prochaine étape sera donc de répéter cette recherche dans d'autres régions pour permettre de confirmer et de mieux quantifier la direction de cette association entre la structure du paysage et les patrons temporels des épidémies. Dans un deuxième temps, des chercheurs peuvent aussi travailler pour mieux comprendre les mécanismes de ces influences à cette échelle. Par exemple, de nouvelles techniques utilisant des marqueurs génétiques peuvent aider à comprendre l'importance de la dispersion des épicentres vers des habitats moins favorables et donc permettraient aussi de comprendre les mécanismes affectant la synchronie des épidémies. Notre étude ne supporte pas l'effet de la proximité des habitats d'espèces hôtes et donc de l'importance de la dispersion, car les sites plus rapprochés ne sont pas nécessairement plus synchrones que les sites éloignés, mais une étude plus en détail de la connectivité du paysage et du synchronisme des épidémies pourrait fournir une réponse permettant de décrire les observations illustrées dans cette thèse. De plus, des données portant sur la structure forestière et ayant une résolution temporelle plus grande que 1975 nous auraient permis de déterminer la relation positive ou négative entre certaines variables décrivant la structure du paysage et la dynamique des épidémies. Il est possible que la dispersion puisse jouer un rôle plus local dans la sévérité des épidémies et la présence ou non d'espèces hôtes peut agir à titre de barrière physique et interférer avec cette dispersion (Jactel and Brockerhoff, 2007; Roth *et al.*, 2006).

Il existe toujours une préoccupation voulant qu'un déclin de la biodiversité ait des répercussions importantes sur la résilience écologique des écosystèmes face aux perturbations futures (Drever *et al.*, 2006; Folke *et al.*, 2004). Certains chercheurs avancent que les écosystèmes riches en espèces végétales sont moins vulnérables aux épidémies des insectes (Cappuccino *et al.*, 1998; Jactel and Brockerhoff, 2007; Root,

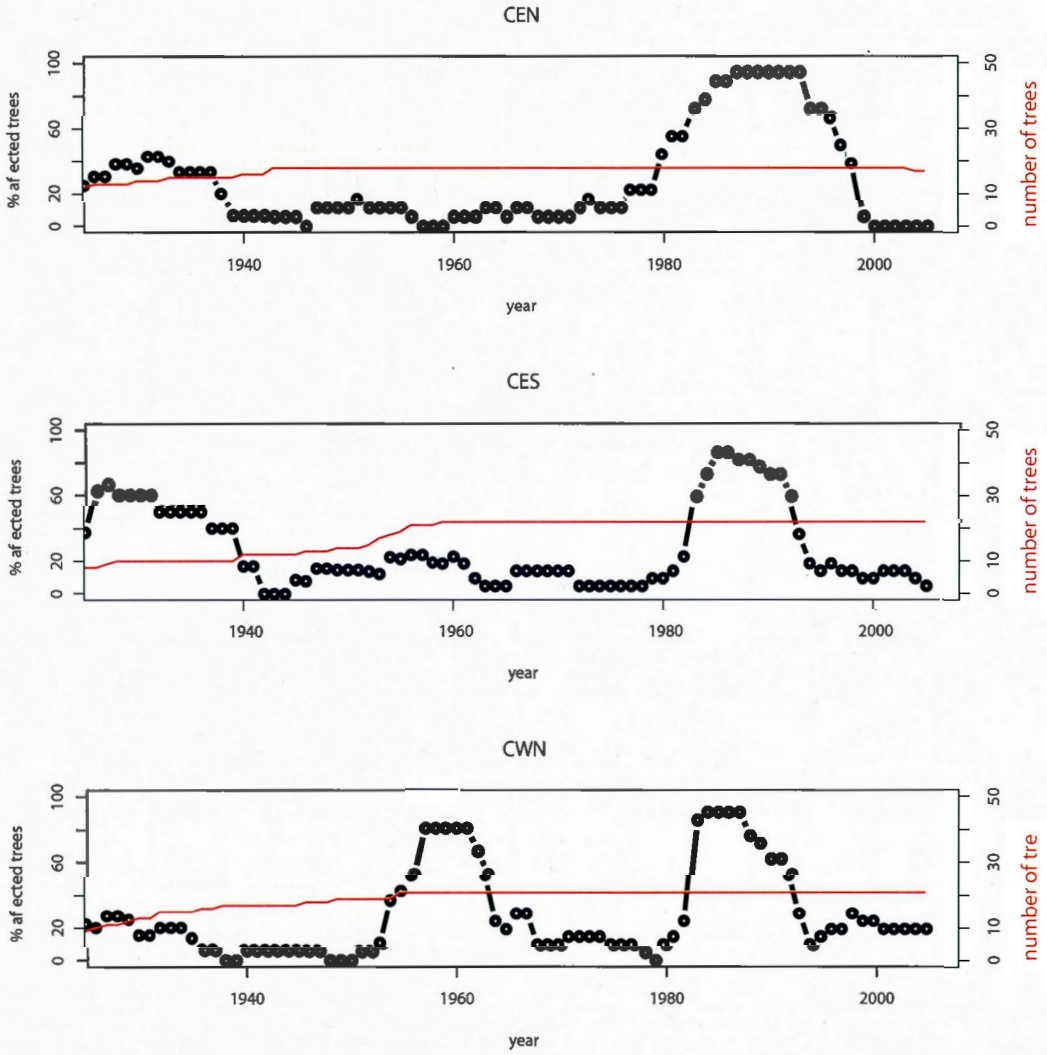
1973), car cette diversité réduit la disponibilité des hôtes et améliore le contrôle des populations par les ennemis naturels. Malgré que cette idée soit toujours débattue (Koricheva *et al.*, 2006), il nous apparaît que les questions portant sur l'effet des changements de la structure et de la composition du paysage forestier par l'aménagement doivent être intégrées autant que possible à la planification forestière concernant la lutte préventive contre les pertes dues aux épidémies d'insectes. Bien qu'il soit impossible de supprimer les épidémies d'insectes, une meilleure planification pourrait permettre de réduire la sévérité ou encore de faciliter des opérations de coupes de récupération. Les outils d'aide à la décision pour minimiser les effets des insectes (MacLean *et al.*, 2000) tiennent compte surtout de la composition et de la structure forestière actuelle et sont basés sur le cumul des caractéristiques à l'échelle du paysage. Notre étude souligne l'importance de considérer l'effet de la structure du paysage dans la planification préventive. L'ensemble de nos résultats montre surtout l'importance de considérer l'effet de l'aménagement forestier sur de multiples insectes (ou autres processus naturels). Par exemple, dans notre étude, la zone de conservation a subi les épidémies de tordeuse des bourgeons d'épinette plus sévères et synchrones, mais des épidémies de livrée des forêts moins synchrones tandis que les zones aménagées ont subi l'inverse. Ces interactions entre perturbations peuvent donc être importantes et créer des effets inattendus s'ils ne sont pas considérés, car une planification ayant pour objectif de diminuer l'influence d'une perturbation peut, par le fait même, avoir un effet amplificateur sur une autre (James *et al.*, 2011).

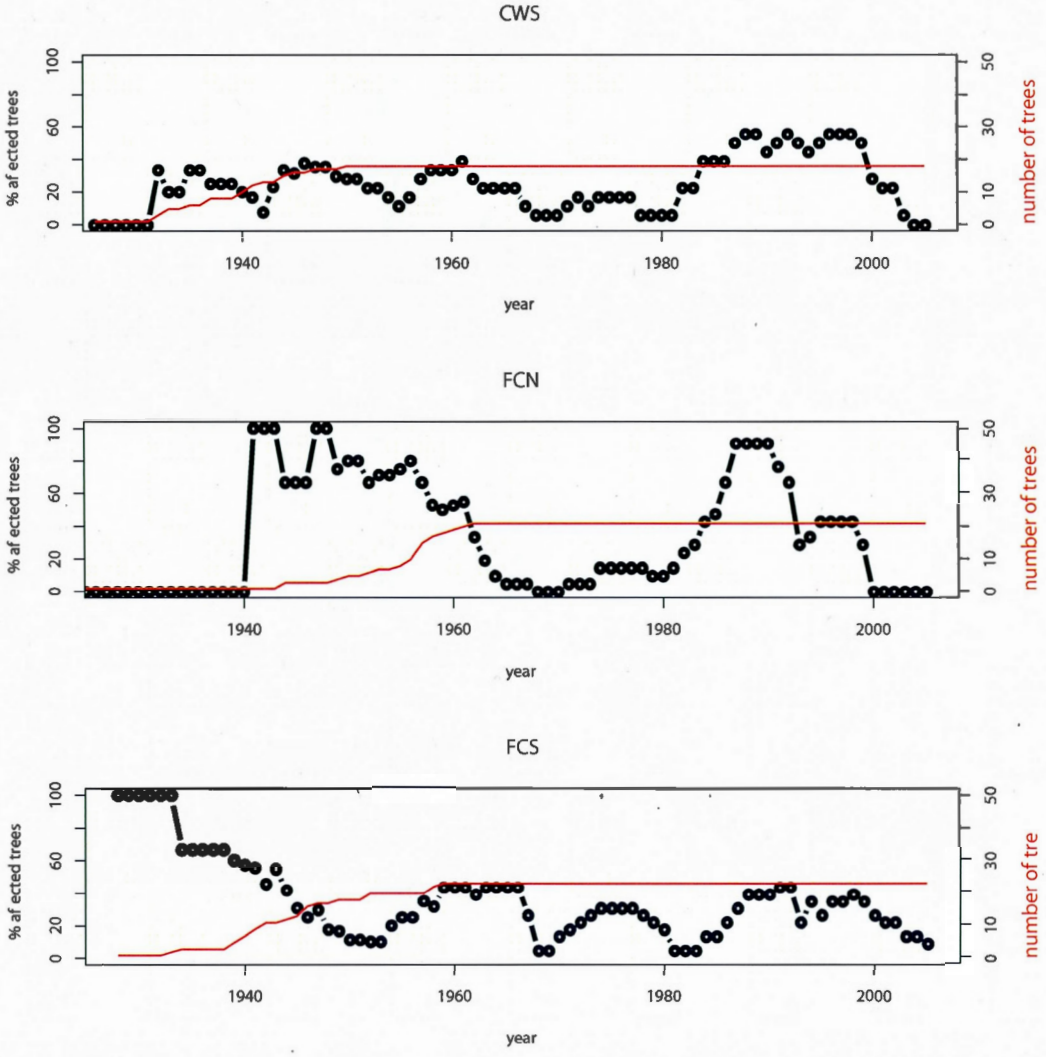
Il convient aussi d'être prudent dans l'interprétation de ces conclusions, car l'influence des legs forestiers à l'échelle du paysage reste encore une question ouverte pour des endroits contenant beaucoup plus de sapins baumiers que notre aire d'étude comme

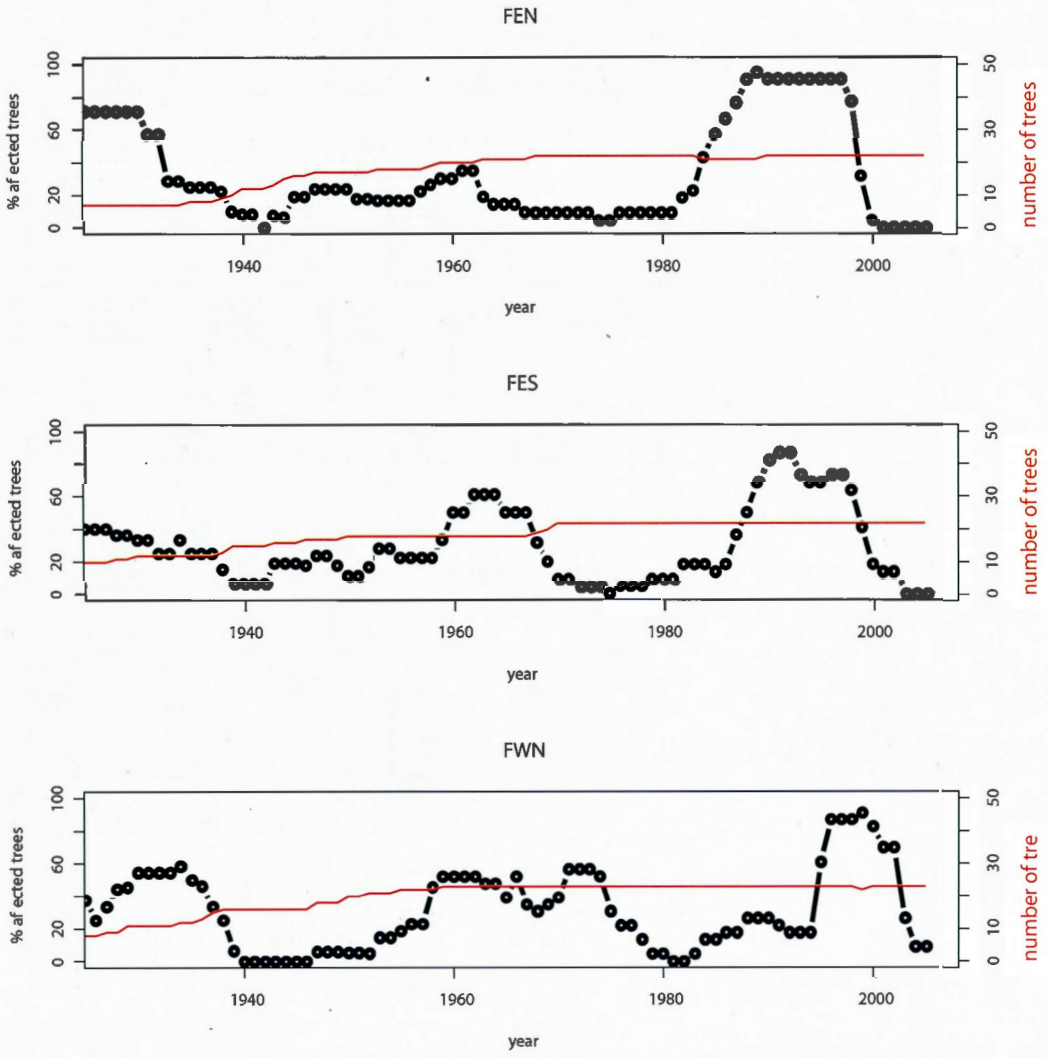
l'est du Canada, où la dynamique forestière est différente et qui pourrait notamment influencer les épidémies de la tordeuse. Il est donc clair que plus d'études seront nécessaires pour bien quantifier l'effet de l'aménagement forestier à l'échelle du paysage. Malgré tout, notre étude démontre clairement que les effets des changements anthropiques associés à l'aménagement forestier à l'échelle du paysage sont réels et qu'il est important de les mesurer dans une variété de conditions forestières.

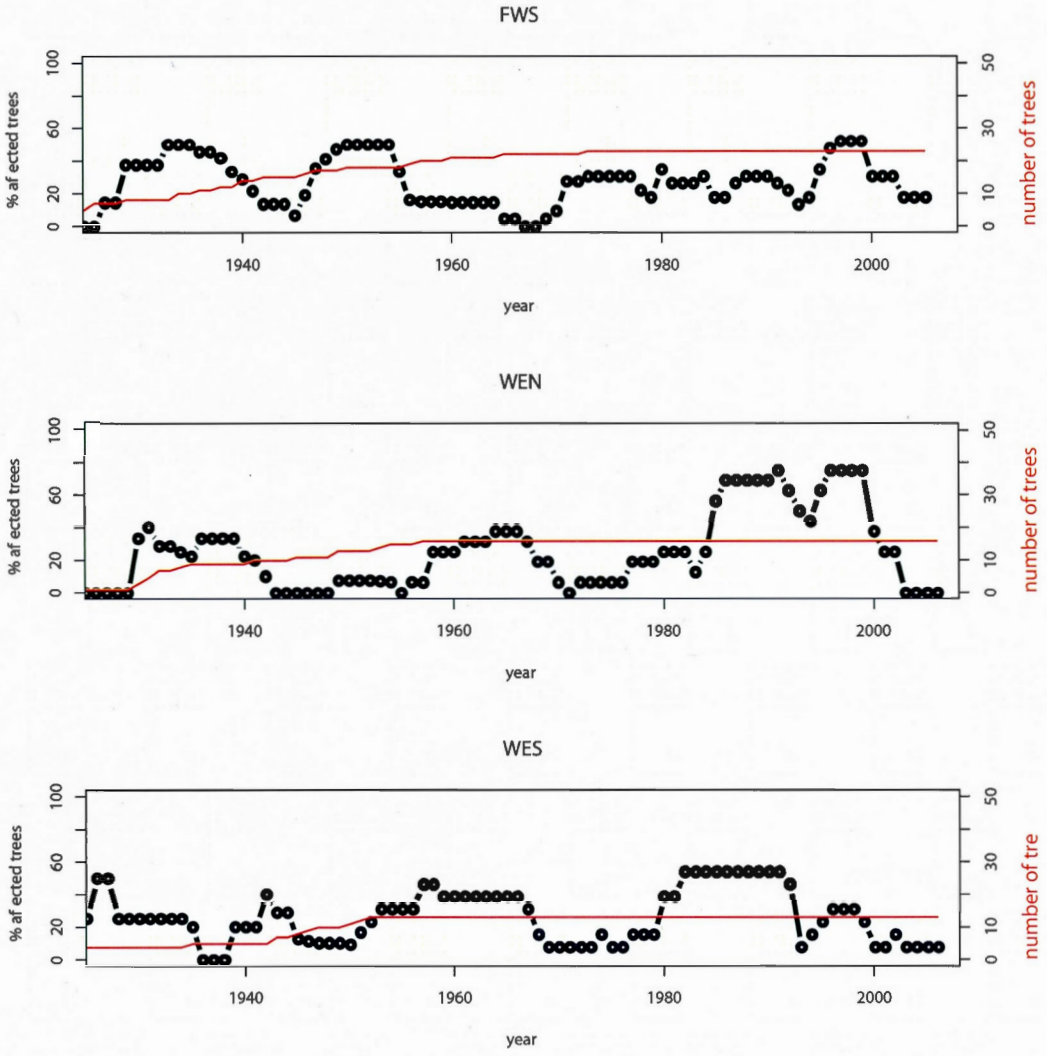
APPENDICE A

OUTBREAK OUTPUT FOR SPRUCE BUDWORM




CWS
% af ected trees
number of trees
year
1940
1960
1980
2000
FCN
% af ected trees
number of trees
year
FCS
% af ected trees
number of tre
year


FEN
% af ected trees
number of trees
year
1940
1960
1980
2000
FES
% af ected trees
number of trees
year
FWN
% af ected trees
number of tre
year


FWS
% af ected trees
number of trees
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% af ected trees
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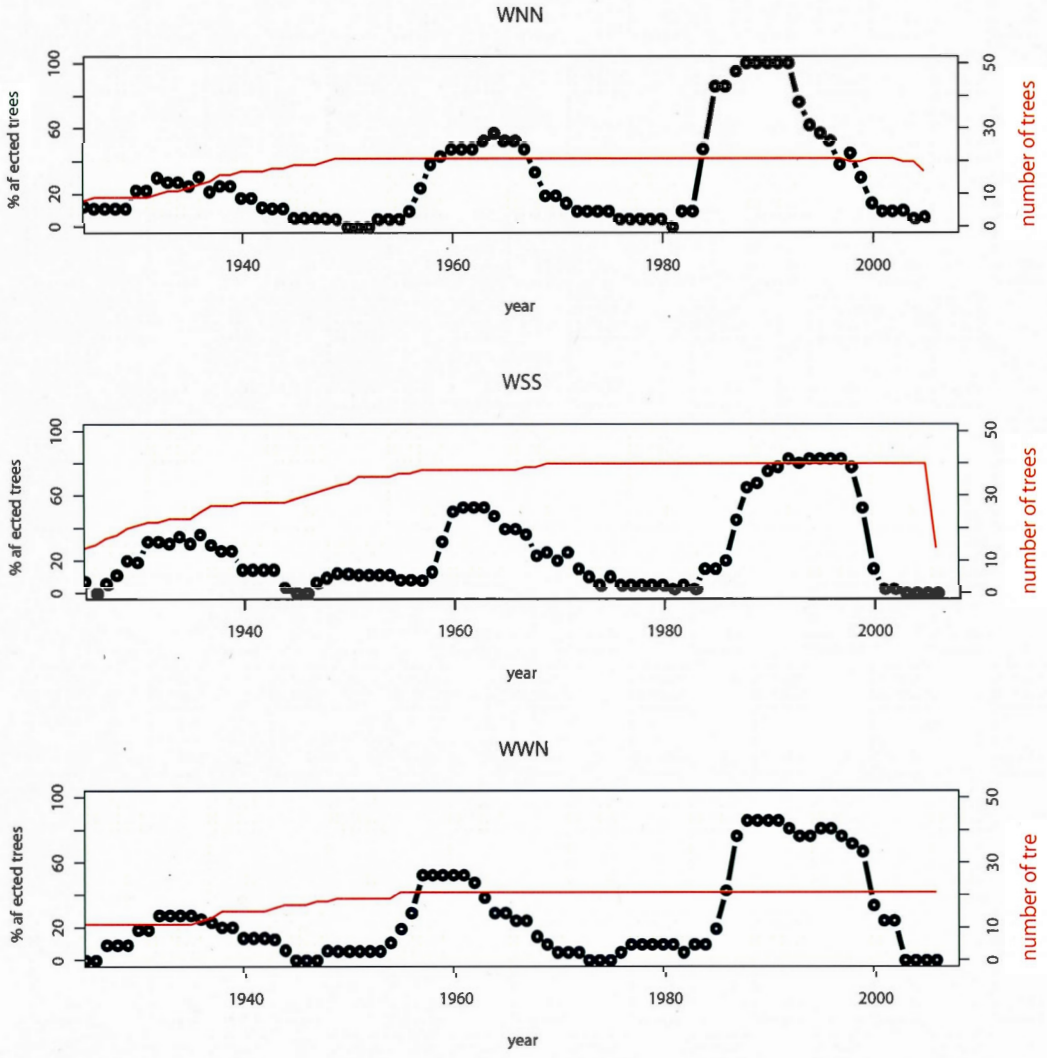
year


WNN
% af ected trees
number of trees
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1940
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WSS
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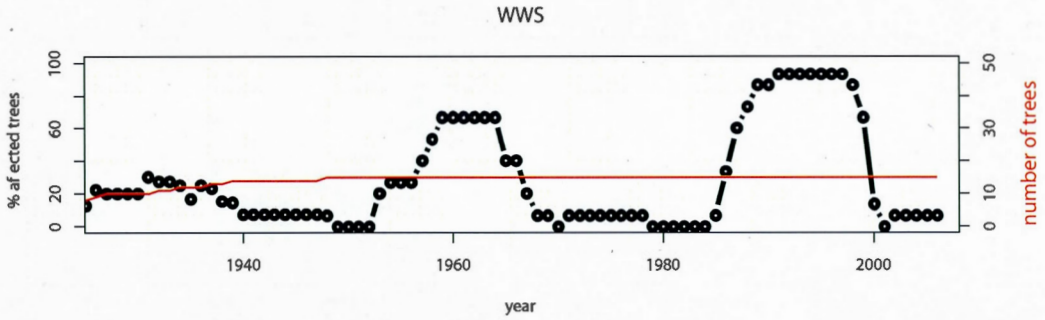
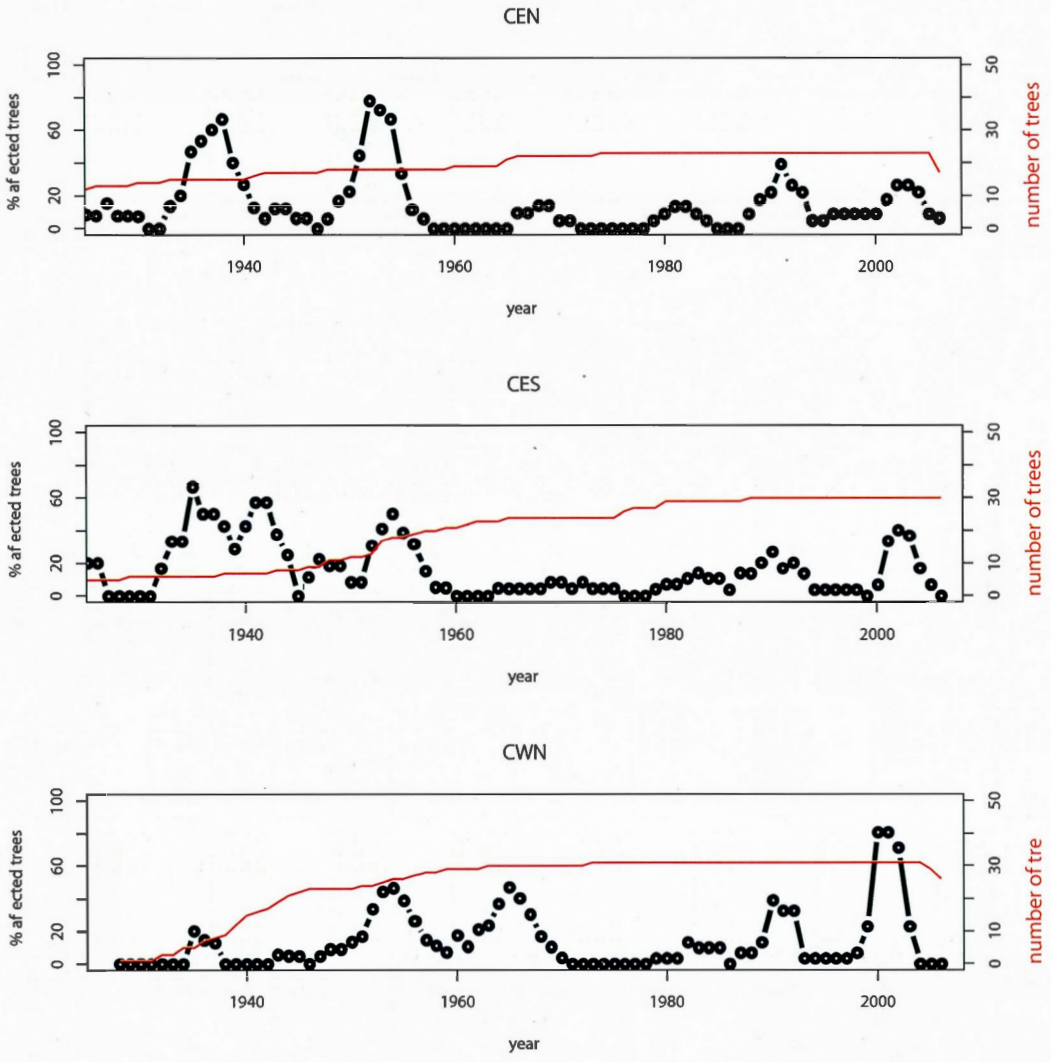
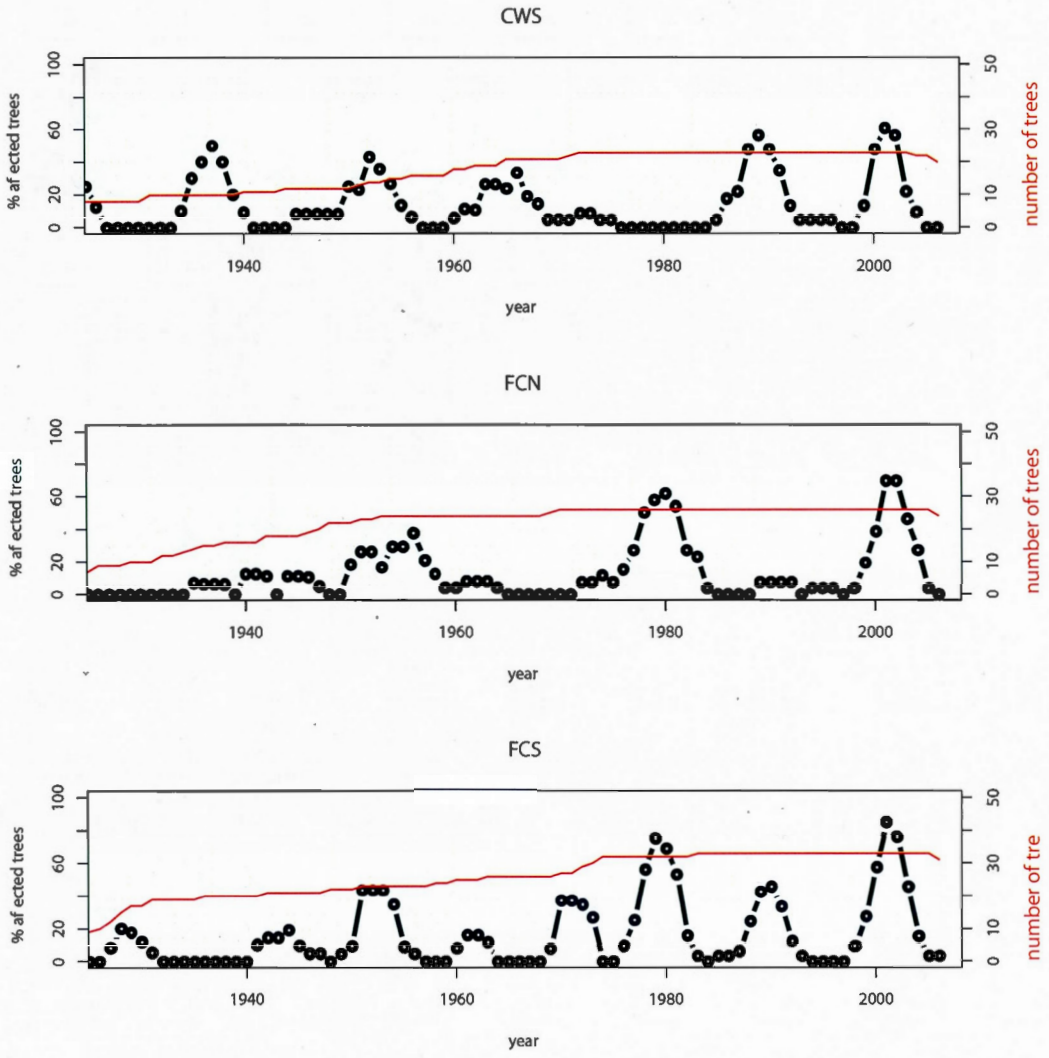

WWS
% af ected trees
0
20
60
100
number of trees
0
10
30
50
1940
1960
1980
2000
year

APPENDICE B

OUTBREAK OUTPUT FOR FOREST TENT CATERPILLAR




CWS
% af ected trees
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number of trees
0
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year
FCN
% af ected trees
0
20
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100
number of trees
0
10
30
50
1940
1960
1980
2000
year
FCS
% af ected trees
0
20
60
100
number of tre
0
10
30
50
1940
1960
1980
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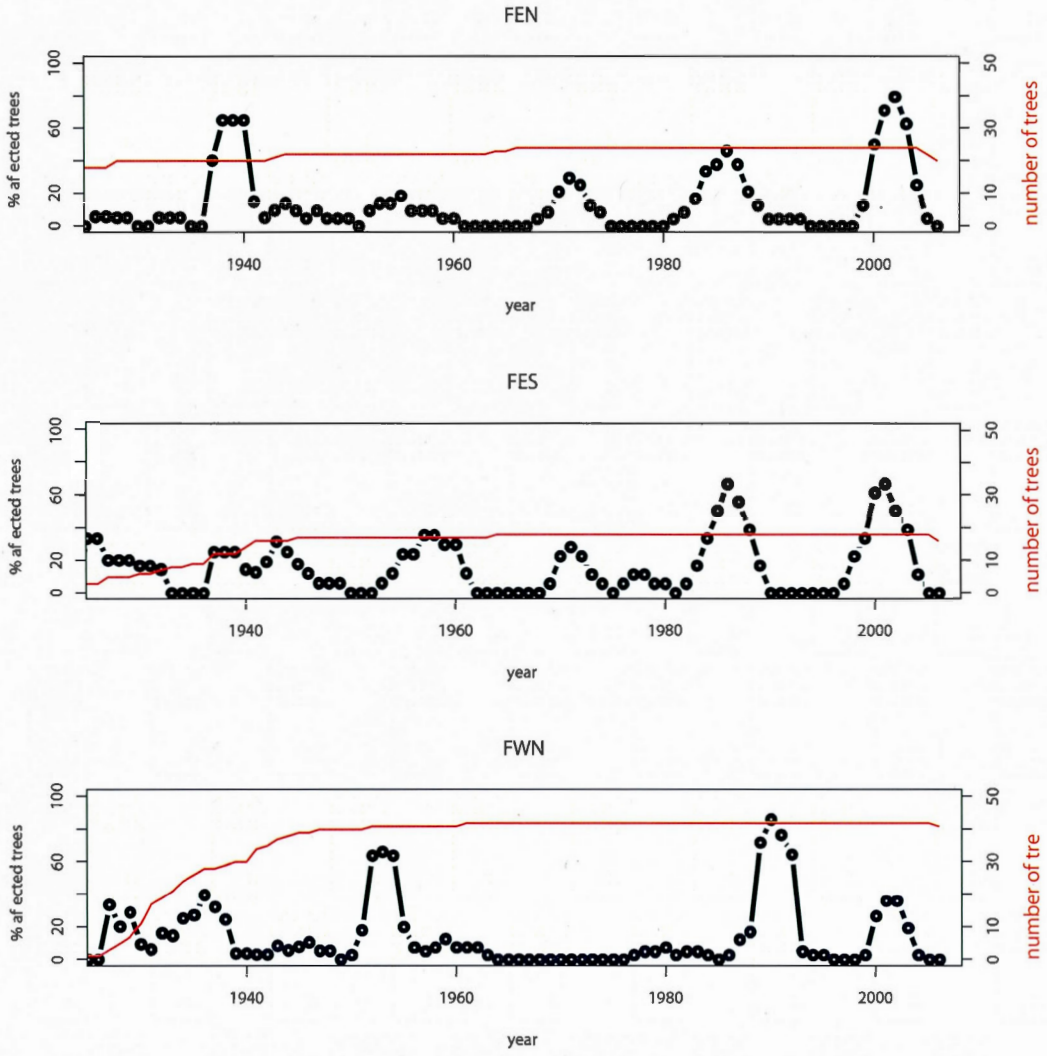
year


FEN
% af ected trees
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20
60
100
number of trees
0
10
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1940
1960
1980
2000
year
FES
% af ected trees
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20
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100
number of trees
0
10
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FWN
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number of tre
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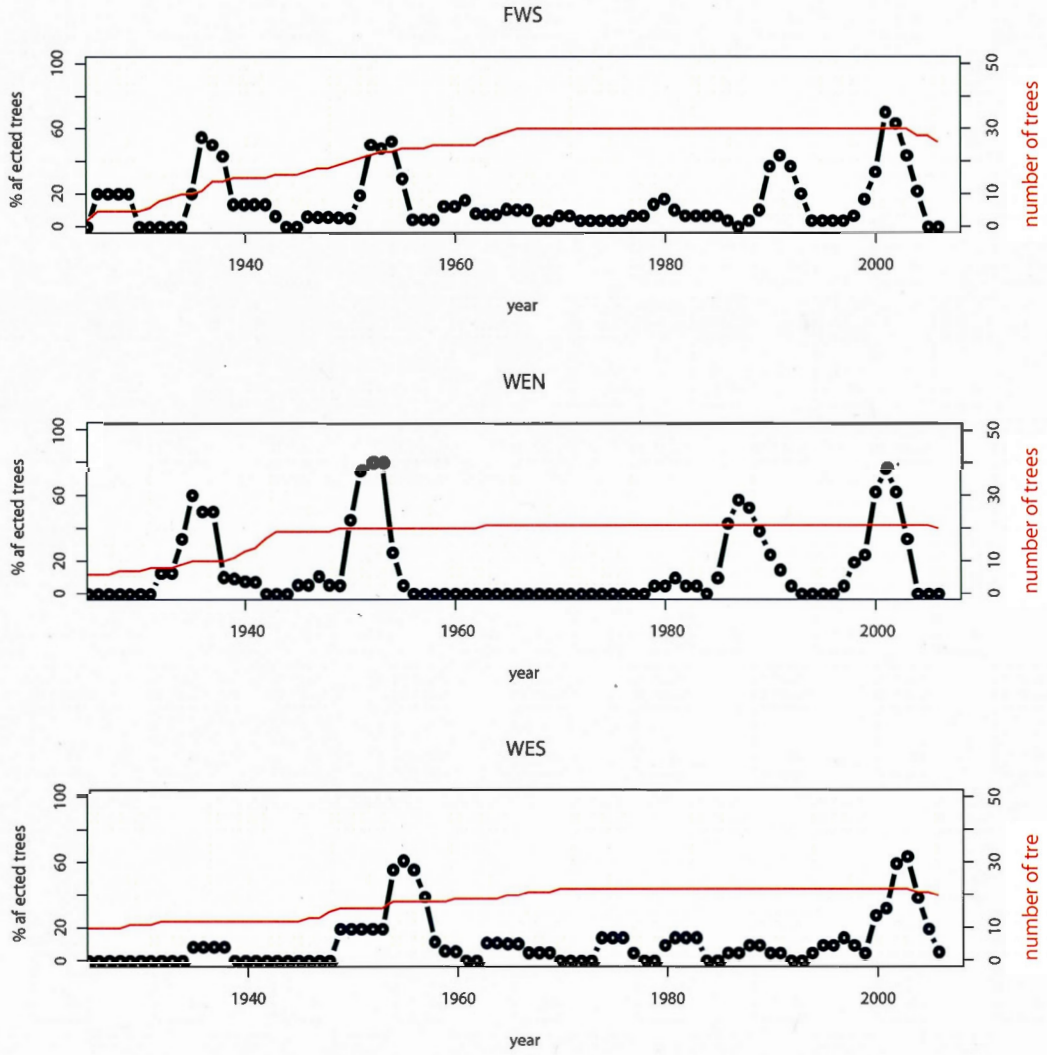
year


FWS
% af ected trees
0
20
60
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number of trees
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10
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1940
1960
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2000
year
WEN
% af ected trees
0
20
60
100
number of trees
0
10
30
50
1940
1960
1980
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year
WES
% af ected trees
0
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number of tre
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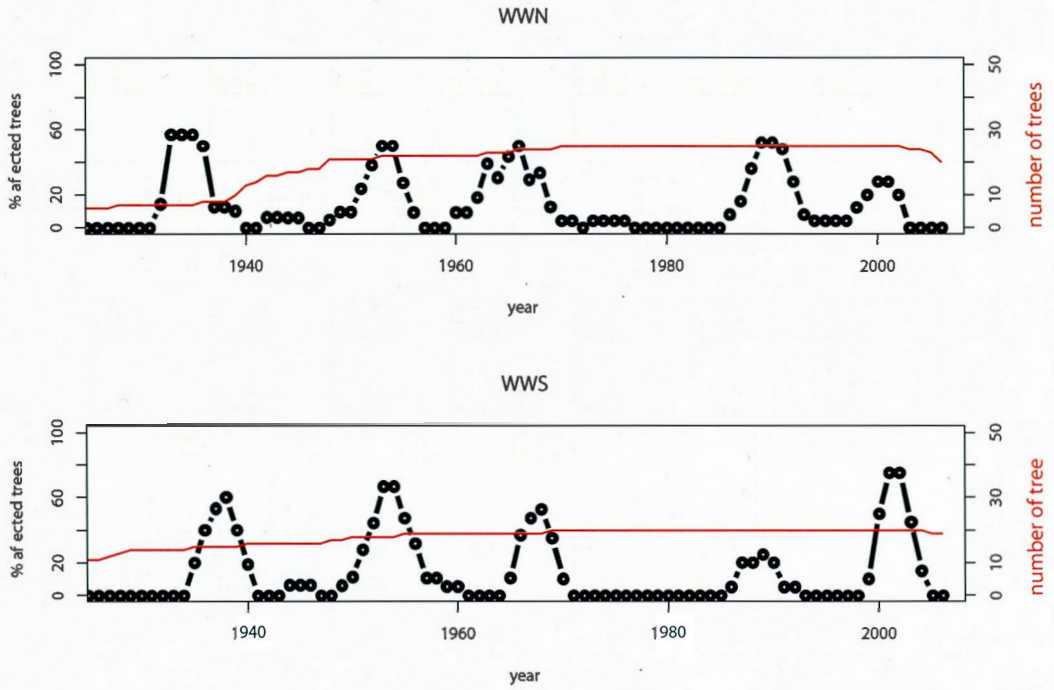
WWN
% af ected trees
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number of trees
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1940
1960
1980
2000
year
WWS
% af ected trees
0
20
60
100
number of tree
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50
1940
1960
1980
2000
year

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